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A REFERENCE LIST OF THE TREMATODE PARASITES OF BRITISH FRESHWATER FISHES.

BY WILLIAM NICOLL, M.A., D.Sc., M.D.,

Medical Officer of Health, South Shields.

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INTRODUCTION.

OUR freshwater fishes have for long been a subject of some economic interest and in consequence their diseases and their parasites have received quite a considerable amount of attention. Much has been written on the subject, even in this country, and it has formed the basis of not a little speculation and possibly some results of economic value. As usual, however, more attention has been devoted to the matter on the continent and in America. It is, nevertheless, gratifying to find that McIntosh (1863) was one of the first to realise the important help to be derived from a scientific study of fish parasites in investigations on such problems as migration, etc. His work has been greatly amplified by the later researches of such men as Hofer (1904) and Zschokke (1884–1914) in Europe, and Ward (1908–11) in America, to mention only a few well-known names which have been prominent in this line of investigation.

The conclusion reached by these investigators is that, apart from the matter of disease-production, information concerning the parasites of freshwater fishes may be useful in helping to elucidate obscure points in our knowledge of the habits and life-histories of their hosts. For that reason, if no other, it seems desirable to concentrate available data for ease in reference.

While not presuming to enter on discussion of the bionomics of freshwater fishes I believe that some comment is necessary on opinions that have been expressed with reference to the light thrown on this subject by a study of their parasites.

The first point that may be noted is that the Trematode fauna of freshwater fishes differs very considerably from that of marine fishes but certain species occur in both, *e.g.* in migratory fishes such as the salmon or in brackish water fishes like the three-spined stickleback.

What may be regarded as the essentially characteristic common Trematodes of freshwater fishes are such species as *Sphaerostoma bramae*, *Allocreadium isoporum*, *Catoptroides macrocotyle*, *Azygia lucii*, *Bucephalus polymorphus*, *Diplostomum cuticola*, *Diplostomum volvens*, *Diplozoon paradoxum*, and *Gyrodactylus elegans*, none of which are parasites of purely marine fishes. It is evident, therefore, that a migrant fish, infected with any of these parasites, must in all probability have acquired its infection while living in fresh water. Now of the fishes which commonly or habitually frequent both salt and fresh water we find that such species as the bass (*Morone labrax*), the flounder (*Pleuronectes flesus*), the shad (*Alosa vulgaris*) and the sturgeon (*Acipenser sturio*) exhibit a Trematode fauna which is exclusively marine in character. The salmon would also be included in this list were it not for the occurrence of the problematical species *Distomum miescheri*, which is certainly not a parasite of any species of British marine fish. It has been recorded in the salmon only once by Zschokke and once by Tosh in the Tweed. The latter identification, however, must be regarded with some doubt.

Again, the smelt (*Osmerus eperlanus*) and the common eel (*Anguilla anguilla*) present a fauna which is preponderantly marine in character, though in the case of the latter such typical freshwater forms as *Sphaerostoma bramae*, *Azygia lucii* and *Bucephalus polymorphos* have been recorded. The fact that it includes amongst its parasites three of the commonest marine forms, namely, *Derogenes varicus*, *Lecithaster gibbosus*, and *Hemiurus communis*, appears to indicate that the eel, at least, feeds equally freely both in salt and fresh water. It, at any rate, does not seek fresh water (or salt water as the case may be) in order to *rid* itself of its parasites for in so doing it merely substitutes a different collection. From this example it is evident that the theory that fishes migrate from salt to fresh water and *vice versa* for the purpose, as has been suggested, of ridding themselves of their parasites cannot be regarded as of general application and must in fact be viewed with much scepticism.

The observation that migrant fishes, in the higher reaches of the river, are relatively or absolutely free from parasitic worms indicates that the change of environment has a deleterious effect on the parasites but it seems altogether too far-fetched to suggest that such effect should be the, or even a, factor in determining migration.

With regard to the distribution of the better known parasites throughout the freshwater fauna a few interesting facts may be indicated. For instance *Sphaerostoma bramae*, the commonest of freshwater fish Trematodes, is essentially a parasite of the Cyprinids and otherwise occurs only in the pike, perch and eel. *Allocreadium isoporum* and *Diplostomum cuticola* are exclusively Cyprinid parasites. The following also are chiefly Cyprinid parasites, viz. *Catoptroides macrocotyle* (also in the perch), *Bucephalus polymorphus* (also in the burbot and the eel) and *Diplozoon paradoxum* (also on the burbot and *Cottus gobio*). On the other hand *Azygia lucii* does not occur in any of the Cyprinids.

Another matter of much interest is the function of freshwater fishes as intermediate hosts of larval Trematodes. Most characteristic perhaps are the larval forms of Hemistomes and Holostomes, referred to under the larval generic names *Diplostomum*, *Tylodelphys* and *Tetracotyle*. Numerous forms of this class are met with in freshwater fishes. They occur in the eye, under the skin or in the muscles or peritoneum. *Tylodelphys* shows a preference for the brain and central nervous system while *Tetracotyle* occurs chiefly in the peritoneum.

Quite a number, however, of encysted larval Distomes also occur in freshwater fishes, and while most of these have not yet been referred to any known adults, several well-known forms have been recognized. Amongst these may be mentioned *Clinostomum complanatum*, *Opisthorchis felineus*, *Metorchis albidus*, *Metagonimus yokogawai* and *Pseudamphistomum danubiense*, some of which are of importance in human and mammalian pathology.

Reference lists of the Trematode parasites of freshwater fishes have previously been published by von Linstow (1878–89) and Lühe (1909). These works would appear to be sufficient for all practical purposes but, unfortunately, on the one hand von Linstow's compendium is now very much out of date and, on the other, Lühe gives no references to the literature. It is with the object of supplementing von Linstow and supplying Lühe's omissions that the following list is submitted for publication. The references cited have been selected as being either the best available or the most readily accessible. For ordinary purposes of identification Lühe's work will usually be found sufficient.

As in so many other branches of Helminthology our authentic knowledge dates essentially from Rudolphi (1808–9), but in the case of the monogenetic forms we are much more indebted to von Nordmann (1832). The pioneer work of these two observers was supplemented to some extent by that of F. S. Leuckart (1828–42) and Dujardin (1845), and was revised and brought up to date by Diesing (1835–58). Diesing's contemporary, Wagener (1857–60), extended von Nordmann's work on the monogenetic forms and his is still perhaps the most outstanding work on that branch of the subject. During the following twenty years the most prominent names were those of Wedl (1857), van Beneden (1861–71) and Taschenberg (1879). The work of the last-mentioned constitutes the most modern authoritative work on monogenetic Trematodes.

It was not until the last quarter of the century that the digenetic forms began to receive their due share of attention. Von Linstow (1877–96) was the first to take up an extended study of the freshwater species, his interest being drawn more particularly to the larval forms occurring encysted in so many freshwater fishes. By far the most elaborate work on the subject, however, is that of Looss (1885–1907) and this work constitutes the best which has been done. Following Looss the most important investigations are those of Hausmann (1896–97), Odhner (1901–11) and Ciurea (1911–15).

LIST OF THE TREMATODE PARASITES OF BRITISH FRESHWATER FISHES, ARRANGED SYSTEMATICALLY.

Order **DIGENEA.**

Sub-order **Prosostomata.**

Super-family DISTOMATA.

Family ALLOCREADIIDAE Stoss.

	AUTHORITY
Genus *Allocreadium* Looss	
1. A. angusticolle (Hausmann)	Hausmann 1896, 1897
2. A. isoporum Looss	Looss 1894, Hausmann 1897
3. A. transversale (Rud.)	Dujardin 1845, Odhner 1901
Genus *Crepidostomum* Braun [=*Stephanophiala* Nicoll]	
4. C. farionis (Müller) [=Stephanophiala laureata (Zed.)]	Blanchard 1891, Nicoll 1909

Family HAPLOPORIDAE Looss.

Genus *Haploporus* Looss	
5. H. lateralis Lss.	Looss 1902 *a*
Genus *Saccocoelium* Looss	
6. S. obesum Lss.	Looss 1902 *a*
Genus *Lecithobotrys* Looss	
7. L. putrescens Lss.	Looss 1902 *a*

Family AZYGIIDAE Odhner.

Genus *Azygia* Looss	
8. A. lucii (Müller) [=A. tereticolle (Rud.)]	Looss 1894, Odhner 1911
9. A. loossii Marsh. and Gilb.	Marshall and Gilbert 1905
10. A. robusta Odhner	Odhner 1911

Family HEMIURIDAE Lühe.

Sub-family *Hemiurinae* Looss.

Genus *Hemiurus* (Rud.)	
11. H. appendiculatus (Rud.)	Odhner 1905, Looss 1907

Sub-family *Sterrhurinae* Looss.

Genus *Lecithochirium* Lühe	
12. L. rufoviride (Rud.)	Lühe 1901, Looss 1907

Sub-family *Lecithasterinae* Odhner.

Genus *Lecithaster* Lühe	
13. L. galeatus Lss.	Looss 1907
14. L. confusus Odh.	Odhner 1905, Looss 1907
15. L. gibbosus (Rud.)	Odhner 1905, Looss 1907

Sub-family *Syncoeliinae* Looss.

Genus *Derogenes* Lühe	
16. D. varicus (Müll.)	Odhner 1905, Johnstone 1907

	Authority
Genus *Pronopyge* Looss	
17. P. ventricosa (Rud.)	Looss 1899, Odhner 1911
18. P. ocreata (Rud.)	Odhner 1905, Looss 1907
Family Bunoderidae Looss.	
Genus *Bunodera* Railliet	
19. B. luciopercae (Müll.) [=B. nodulosa (Zed.)]	Looss 1894, Lühe 1909
Family Gorgoderidae Looss.	
Genus *Phyllodistomum* Braun	
20. P. folium (v. Olfers)	v. Olfers 1816, Looss 1894
21. P. conostomum (Olsson)	Olsson 1876, Looss 1902 *c*
Genus *Catoptroides* Odhner	
22. C. macrocotyle Lühe	Lühe 1909
Family Opisthorchiidae Braun.	
Genus *Opisthorchis* R. Blanchard	
23. O. felineus (Riv.)	Askanazy 1906, Ciurea 1915 *b*
Genus *Metorchis* Looss	
24. M. albidus (Brn.)	Stiles and Hassall 1894, Ciurea 1915 *b*
Family Heterophyidae Looss.	
Genus *Metagonimus* Katsurada [=*Loossia* Ciurea]	
25. M. yokogawai Katsurada [=Loossia romanica Ciurea] [=Loossia parva Ciurea]	Ciurea 1915 *a*, Yokogawa 1913
Family Clinostomidae Lühe.	
Genus *Clinostomum* Leidy	
26. C. complanatum (Rud.)	Braun 1900, Ciurea 1911
Unclassified Genera.	
Genus *Asymphlodora* Looss	
27. A. exspinosa (Hausmann)	Hausmann 1897, Looss 1899
28. A. ferruginosa (v. Linst.)	v. Linstow 1877
29. A. tincae (Modeer) [=A. perlata (Nordm.)]	Looss 1894, Mühling 1898
30. A. imitans (Mühling)	Mühling 1898
Genus *Centrovarium* Stafford	
31. C. lobotes (MacCallum)	MacCallum 1895, Stafford 1904
Genus *Haplosplanchnus* Looss	
32. H. pachysomus (Eysenh.)	Eysenhardt 1829, Looss 1902 *b*
Genus *Heterostoma* Filippi	
33. H. luteum (Baer) [=H. ovatum Dies.]	Baer 1827, Ercolani 1881 Gamble 1896
Genus *Sanguinicola* Plehn	
34. S. armata Plehn	Plehn 1908, Odhner 1911
35. S. inermis Plehn	Plehn 1908, Odhner 1911
Genus [*Sinistroporus* Stafford]	
36. S. simplex (Rud.)	Levinsen 1881, Stafford 1904

	Authority
Genus *Sphaerostoma* Rud.	
37. S. bramae (Müller) [=S. globiporum Rud.]	v. Linstow 1882, Looss 1885, 1894

Unclassified Species.

38. Distomum annuligerum Nordm. (larva)	Nordmann 1832, Moulinié 1856
39. D. bliccae v. Linst. (larva)	v. Linstow 1877
40. D. catervarium Looss	Looss 1896
41. D. embryo Olfers (larva)	Olfers 1816, Cobbold 1879
42. D. esocis lucii Rud.	Rudolphi 1809
43. D. inerme v. Linst.	v. Linstow 1879
44. D. musculorum percae Waldenburg	Waldenburg 1860
45. D. phoxini v. Linst. (larva)	v. Linstow 1896
46. D. punctum Zed.	Zeder 1800, Bremser 1824
47. D. roseum v. Ben.	v. Beneden 1871, v. Linstow 1878
48. D. semiflavum v. Linst.	v. Linstow 1880, Stossich 1886
49. D. seriale Rud.	Rudolphi 1808, Dujardin 1845

Super-family MONOSTOMATA.

Genus *Monostomum* Zeder	
50. M. cochleariforme Rud.	Rudolphi 1809, Monticelli 1892
51. "M." constrictum Dies.	Diesing 1855, Monticelli 1892
52. M. cotti v. Linstow	v. Linstow 1889, Monticelli 1892

Super-family HOLOSTOMATA.

Genus *Tetracotyle* Filippi	
53. T. echinata Dies.	Diesing 1858, Braun 1892
54. T. ovata v. Linst.	v. Linstow 1877, Villot 1898
55. T. percae-fluviatilis Moul.	Moulinié 1856, v. Linstow 1877
56. T. phoxini Faust	Mataré 1910, Faust 1918
57. T. typica Dies.	Diesing 1858, v. Linstow 1894
Genus *Diplostomum* v. Nordmann	
58. D. brevicaudatum (Nordm.)	v. Nordmann 1832, Diesing 1850
59. D. cobitidis (v. Linst.)	v. Linstow 1890, Braun 1891
60. D. cuticola (Nordm.)	Villot 1898, Linton 1898
61. D. musculicola (Waldenburg)	Braun 1892, Villot 1898
62. D. parvulum Staff.	Stafford 1904
63. D. volvens Nordm.	v. Nordmann 1832, Fraipont 1880, Gamble 1896
Genus *Tylodelphys* Diesing	
64. T. clavata (Nordm.)	v. Nordmann 1832, Diesing 1850
65. (T.) petromyzontis Brown	Brown 1899
Genus *Holostomum* Nitzsch	
66. H. pellucidum Schlotth.	Schlotthauber 1860

Super-family ASPIDOCOTYLEA.

Genus *Aspidogaster* Baer	
67. A. limacoides Dies.	Diesing 1835, Monticelli 1892

Sub-order **Gasterostomata.**

Family BUCEPHALIDAE Poche.

	AUTHORITY
Genus *Bucephalus* Baer	
68. B. polymorphus (Baer)	Wagener 1857, Ziegler 1883
[=Gasterostomum fimbriatum v. Sieb]	Hausmann 1897
Genus "*Neuronaia*" Goodsir	
69. N. lampetrae Gulliver	Gulliver 1872, Brown 1899

Order **MONOGENEA.**

Family TRISTOMIDAE Cobbold.

Genus *Trochopus* Diesing	
70. T. brauni Mola	Mola 1912
71. T. zschokkei Mola	Mola 1912

Family OCTOCOTYLIDAE v. Ben. and Hesse.

Genus *Discocotyle* Diesing	
72. D. sagittata (F. S. Leuck.)	Leuckart 1842, Diesing 1850
Genus *Mazocraes* Hermann	
73. M. alosae Herm.	v. Beneden 1861, Taschenberg 1879
[=Octobothrium lanceolatum F. S. Leuck.]	
Genus *Ophicotyle* v. Ben. and Hesse	
74. O. fintae v. Ben. and Hesse	v. Beneden and Hesse 1864, Taschenberg 1879
Genus *Diplozoon* Nordmann	
75. D. paradoxum Nordm.	Wagener 1857, v. Beneden 1861, Zeller 1872, Gamble 1896

Family GYRODACTYLIDAE Cobbold.

Genus *Gyrodactylus* Nordmann	
76. G. elegans Nordm.	Wagener 1860, v. Beneden 1861, Kathariner 1894, 1904
77. G. gracilis Kathar.	Kathariner 1894
78. G. medius Kathar.	Kathariner 1894
79. G. rarus Wegener	Wegener 1909
Genus *Dactylogyrus* Diesing	
80. D. amphibothrium Wag.	Wagener 1857, v. Linstow 1878
81. D. auricularis (Nordm.)	Wedl 1857, v. Beneden 1861
82. D. anchoratus Duj.	Dujardin 1845, Wagener 1857
83. D. alatus v. Linst.	v. Linstow 1878
84. D. crucifer Wag.	Wagener 1857, Taschenberg 1879
85. D. difformis Wag.	Wagener 1857, Taschenberg 1879
86. D. dujardinianus Dies.	Dujardin 1845, Diesing 1850
[=D. auriculatus (Dies.) Duj.]	
87. D. fallax Wag.	Wagener 1857, Taschenberg 1879
88. D. major Wag. [nom. nud.]	Wagener 1857, Taschenberg 1879
89. D. malleus v. Linst.	v. Linstow 1877, Sramek 1901
90. D. minor Wag.	Wagener 1857, v. Linstow 1878
91. D. mollis (Wedl)	Wedl 1857, v. Linstow 1885
92. D. tenuis Wedl	Wedl 1857, Taschenberg 1879
93. D. trigonostoma Wag. [nom. nud.]	Wagener 1857, Taschenberg 1879
94. D. tuba v. Linst.	v. Linstow 1878

	Authority
Genus *Ancyrocephalus* Creplin [=*Tetraonchus* Diesing]	
95. A. borealis (Olsson)	Olsson 1893, Pratt 1900
96. A. forceps (Leuck.)	Leuckart 1857, v. Linstow 1878
97. A. monenteron (Wag.)	Wagener 1857, Taschenberg 1879, Pratt 1900
98. A. paradoxus Creplin [=Tetraonchus unguiculatus Dies.]	Diesing 1858, Monticelli 1892

LIST OF THE TREMATODE PARASITES, ARRANGED ACCORDING TO THEIR HOSTS.

ACANTHOPTERYGII

1. *Cottus gobio* Linn. Miller's thumb

Allocreadium angusticolle (Hausm.)	Intestine
Phyllodistomum folium (Olf.)	Urinary bladder
Distomum sp. (larva)	Sub-peritoneum in cysts
Monostomum cotti Linst.	Sub-peritoneum in cysts
Diplozoon paradoxum Nordm.	Gills

2. *Acerina cernua* Linn. Ruffe

Bunodera luciopercae (Müll.)	Intestine
Phyllodistomum folium (Olf.)	Urinary bladder
Sphaerostoma bramae (Müll.)	Intestine
Distomum embryo (Olf.) (larva)	Sub-peritoneum in cysts
Tetracotyle echinata Dies.	Sub-peritoneum in cysts
Tetracotyle ovata Linst.	Sub-peritoneum in cysts
Diplostomum volvens Nordm.	Eye
Tylodelphys clavata Nordm.	Eye
Dactylogyrus amphibothrium Wag.	Gills

3. *Perca fluviatilis* Linn. Perch

Azygia lucii (Müll.)	Intestine
? Hemiurus appendiculatus (Rud.)	Intestine
Bunodera luciopercae (Müll.)	Intestine
Clinostomum complanatum (Rud.) (larva)	Muscles in cysts
Sphaerostoma bramae (Müll.)	Intestine
Distomum annuligerum Nordm. (larva)	Eye
Distomum embryo (Olfers) (larva)	Sub-peritoneum in cysts
Distomum musculorum-percae Waldbg. (larva)	Muscles in cysts
Tetracotyle percae-fluviatilis Moulinié	Peritoneum in cysts
Diplostomum brevicaudatum (Nordm.)	Eye
Diplostomum volvens Nordm.	Eye
Tylodelphys clavata Nordm.	Eye
Bucephalus polymorphus (Baer)	Intestine
Dactylogyrus auricularis Nordm.	Gills
Dactylogyrus tenuis (Wedl)	Gills
Ancyrocephalus paradoxus Crepl.	Gills

4. *Mugil auratus* Risso. Golden grey mullet

Haploporus lateralis Lss.	Intestine
Saccocoelium obesum Lss.	Intestine
Lecithobothrys putrescens Lss.	Intestine
Lecithaster galeatus Lss.	Intestine
Haplosplanchnus pachysomus (Eysenh.)	Intestine

ACANTHOPTERYGII

5. *Pygosteus pungitius* Linn. Ten-spined stickleback

Gyrodactylus rarus Wegen.	Skin

ANACANTHINI

6. *Lotta lota* Linn. Burbot

Azygia lucii (Müll.)	Stomach and mouth
? Hemiurus appendiculatus (Rud.)	Stomach and intestine
? Sinistroporus simplex (Rud.)	Intestine
Diplostomum volvens Nordm.	Eye
Tylodelphys clavata Nordm.	Eye
Bucephalus polymorphus Baer	Intestine
Diplozoon paradoxum Nordm.	Gills
Gyrodactylus sp.	Skin and gills

PHYSOSTOMI

7. *Cyprinus carpio* Linn. Common carp

Allocreadium isoporum Lss.	Intestine
Sphaerostoma bramae (Müll.)	Intestine
Sanguinicola inermis Plehn	Blood vessels
Tetracotyle sp.	In cysts on intestine
Diplostomum cuticola (Nordm.)	In cysts under skin
Gyrodactylus elegans Nordm.	Skin and gills
Gyrodactylus medius Kath.	Skin and gills
Gyrodactylus gracilis Kath.	Skin and gills
Dactylogyrus anchoratus Duj.	Gills
Dactylogyrus mollis (Wedl)	Gills
Dactylogyrus auricularis Nordm.	Gills
Dactylogyrus dujardinianus Dies.	Gills

8. *Carassius carassius* Linn. Crucian carp

Catoptroides macrocotyle Lühe	Ureters
Metagonimus yokogawai Kats.	Intestine
Diplozoon paradoxum Nordm.	Gills
Gyrodactylus sp.	Skin and gills
Dactylogyrus dujardinianus Dies.	Gills

9. *Barbus barbus* Linn. Barbel

Allocreadium isoporum Lss.	Intestine
Bunodera luciopercae (Müll.)	Intestine
Catoptroides macrocotyle Lühe	Ureters
Asymphlodora exspinosa (Hausm.)	Intestine
Asymphlodora ferruginosa (Linst.)	Intestine
Sphaerostoma bramae (Müll.)	Intestine
Distomum punctum Zed.	Intestine
Monostomum cochleariforme Rud.	Intestine
Diplostomum brevicaudatum Nordm.	Eye
Dactylogyrus malleus Linst.	Gills

10. *Gobio gobio* Linn. Gudgeon

Catoptroides macrocotyle Lühe	Ureters
Diplostomum cuticola (Nordm.)	Cysts under skin
Bucephalus polymorphus Baer	Intestine
Trochopus brauni Mola	Skin
Trochopus zschokkei Mola	Skin
Diplozoon paradoxum Nordm.	Gills

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10. *Gobio gobio* Linn.	
Gyrodactylus gracilis Kath.	Gills
? Dactylogyrus major Wag.	Gills
11. *Rutilus rutilus* Linn. Roach	
Allocreadium isoporum Lss.	Intestine
Catoptroides macrocotyle Lühe	Ureters
Opisthorchis felineus (Riv.) (larva)	Muscles in cysts
Metorchis albidus (Brn.) (larva)	Muscles in cysts
Sphaerostoma bramae (Müll.)	Intestine
Diplostomum volvens Nordm.	Eye
Diplostomum cuticola (Nordm.)	Cysts under skin
Diplozoon paradoxum Nordm.	Gills
Gyrodactylus elegans Nordm.	Skin and gills
Dactylogyrus crucifer Wag.	Gills
Dactylogyrus fallax Wag.	Gills
Dactylogyrus dujardinianus Dies.	Gills
Dactylogyrus trigonostoma Wag.	Gills
12. *Scardinius erythrophthalmus* Linn. Rudd	
Catoptroides macrocotyle Lühe	Ureters
Metagonimus yokogawai Kats. (larva)	Muscles in cysts
Sphaerostoma bramae (Müll.)	Intestine
Sanguinicola inermis Plehn	Blood vessels
Diplostomum volvens Nordm.	Eye
Diplostomum cuticola (Nordm.)	Under skin in cysts
Diplostomum musculicola (Waldbg.)	Muscles in cysts
Bucephalus polymorphus Baer (larva)	Under skin in cysts
Diplozoon paradoxum Nordm.	Gills
Gyrodactylus gracilis Kath.	Skin and gills
Dactylogyrus crucifer Wag.	Gills
Dactylogyrus difformis Wag.	Gills
Dactylogyrus fallax Wag.	Gills
13. *Leuciscus leuciscus* Linn. Dace	
Sphaerostoma bramae (Müll.)	Intestine
Bucephalus polymorphus Baer (larva)	Under skin in cysts
? Gyrodactylus elegans Nordm.	Ventral fins
Dactylogyrus tuba Linst.	Gills
14. *Leuciscus cephalus* Linn. Chub	
Allocreadium isoporum Lss.	Intestine
Azygia tereticollis (Rud.)	Intestine
Catoptroides macrocotyle Lühe	Ureters
Sphaerostoma bramae (Müll.)	Intestine
Tetracotyle sp.	Intestinal wall and muscles in cysts
Diplostomum cuticola Nordm.	Under skin in cysts
Aspidogaster limacoides Dies.	Intestine
Dactylogyrus tuba Linst.	Gills
Ancyrocephalus forceps (Leuck.)	Gills
15. *Phoxinus phoxinus* Linn. Minnow	
Allocreadium isoporum Lss.	Intestine
Sphaerostoma bramae (Müll.)	Intestine
Distomum phoxini Linst. (larva)	In cysts

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15. *Phoxinus phoxinus* Linn.

Tetracotyle phoxini Faust	Brain
Diplostomum volvens (Nordm.)	Eye
Diplostomum cuticola (Nordm.)	Subcutaneous cysts
Tylodelphys clavata (Nordm.)	Eye
Diplozoon paradoxum Nordm.	Gills
? Gyrodactylus elegans Nordm.	Gills
Dactylogyrus auricularis (Nordm.)	Gills

16. *Tinca tinca* Linn. Tench

Allocreadium isoporum Lss.	Intestine
Opisthorchis felineus (Riv.) (larva)	In cysts
Pseudamphistomum danubiense Ciurea (larva)	In cysts
Sphaerostoma bramae (Müll.)	Intestine
Sanguinicola armata Plehn	Blood vessels
Asymphlodora tincae (Modeer)	Intestine
Gyrodactylus sp.	Skin and gills

17. *Abramis brama* Linn. Common bream

Allocreadium isoporum Lss.	Intestine
Metagonimus yokogawai (Kats.) (larva)	In cysts
Asymphlodora imitans (Mühling)	Intestine
Asymphlodora ferruginosa (Linst.)	Intestine
Catoptroides macrocotyle Lühe	Ureters
Sphaerostoma bramae (Müll.)	Intestine
"Monostomum" constrictum Dies.	Eye
Tetracotyle ovata Linst.	Peritoneum in cysts
Diplostomum cuticola (Nordm.)	Subcutaneous cysts
Diplostomum musculicola Waldbg.	Muscles in cysts
Diplozoon paradoxum Nordm.	Gills
? Gyrodactylus elegans Nordm.	Gills
Dactylogyrus auricularis (Nordm.)	Gills
Dactylogyrus dujardinianus Dies.	Gills

18. *Blicca björkna* Linn. White bream

Metagonimus yokogawai (Kats.) (larva)	In cysts
Catoptroides macrocotyle Lühe	Ureters
Sphaerostoma bramae (Müll.)	Intestine
Distomum bliccae Linst. (larva)	Muscles in cysts
Tetracotyle ovata Linst.	Peritoneum in cysts
Diplostomum cuticola (Nordm.)	Subcutaneous cysts
Bucephalus polymorphus Baer (larva)	Subcutaneous cysts
Diplozoon paradoxum Nordm.	Gills
Dactylogyrus alatus Linst.	Gills
Dactylogyrus minor Wag.	Gills

19. *Alburnus alburnus* Linn. Bleak

Sphaerostoma bramae (Müll.)	Intestine
Bucephalus polymorphus Baer (larva)	Gills
Diplozoon paradoxum Nordm.	Gills
Gyrodactylus sp.	Skin and gills
Dactylogyrus alatus Linst.	Gills
Dactylogyrus minor Wag.	Gills

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20. *Nemachilus barbatula* (Linn.). Loach	
Sphaerostoma bramae (Müll.)	Intestine
Distomum sp. (larva)	Peritoneum in cysts
Monostomum sp. (larva)	? Intestine in cysts
Tetracotyle sp. (Hausmann)	Intestine
Diplostomum cobitidis (Linst.)	Peritoneum in cysts
? Gyrodactylus elegans Nordm.	Gills and fins
21. *Cobitis taenia* Linn. Spined loach	
Allocreadium transversale (Rud.)	Intestine
Diplostomum cuticola (Nordm.)	Peritoneum in cysts
22. *Esox lucius* Linn. Pike	
Allocreadium isoporum Lss.	Intestine
Azygia lucii (Müll.)	Stomach
Azygia loossii Marshall and Gilbert	Stomach
? Hemiurus appendiculatus Rud.	Stomach and intestine
Bunodera luciopercae (Müll.)	Intestine
Phyllodistomum folium (Olfers)	Urinary bladder
Centrovarium lobotes (MacCallum)	Stomach
Sphaerostoma bramae (Müll.)	Intestine
Heterostoma luteum (Baer)	Intestine
Metagonimus yokogawai (Kats.) (larva)	In cysts
Distomum esocis lucii Rud.	Intestine
Bucephalus polymorphus Baer	Intestine
Diplostomum parvulum Staff.	Intestine in cysts
Tylodelphys clavata (Nordm.)	Eye
Gyrodactylus elegans Nordm.	Gills
Ancyrocephalus monenteron (Wag.)	Gills
23. *Salmo fario* Linn. River trout	
Crepidostomum farionis (Müll.)	Intestine
Azygia lucii (Müll.)	Stomach
? Hemiurus appendiculatus (Rud.)	Stomach
Distomum sp. (larva)	Orbit in cysts
Discocotyle sagittata (Leuck.)	Gills
Gyrodactylus sp.	Gills and skin
24. *Salvelinus salvelinus* Linn. Char	
Crepidostomum farionis (Müll.)	Intestine
Azygia lucii (Müll.)	Stomach
Phyllodistomum folium (Olfers)	Urinary bladder
? Distomum seriale Rud.	Kidneys
25. *Coregonus oxyrhynchus* Linn. Houting	
Crepidostomum farionis (Müll.)	Intestine
? Hemiurus appendiculatus Rud.	Intestine
? Derogenes varicus (Zed.)	Intestine
Phyllodistomum conostomum (Olsson)	Oesophagus, gills
Discocotyle sagittata (Leuck.)	Gills
26. *Thymallus thymallus* Linn. Grayling	
Crepidostomum farionis (Müll.)	Intestine
Azygia lucii (Müll.)	Intestine
Phyllodistomum folium (Olfers)	Intestine
Derogenes varicus (Zed.)	Intestine

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26. *Thymallus thymallus* Linn.	
Discocotyle sagittata (Leuck.)	Gills
Ancyrocephalus borealis (Olsson)	Gills
27. *Clupea finta* Cuv. Twaite shad	
Pronopyge ventricosa (Rud.)	Stomach
Pronopyge ocreata (Rud.)	Intestine
Hemiurus appendiculatus (Rud.)	Stomach
Lecithaster confusus Odhner	Rectum
Mazocraes alosae Hermann	Gills
Ophicotyle fintae v. Ben. and Hesse	Gills
28. *Lampetra fluviatilis* Linn. River lamprey	
? Hemiurus appendiculatus (Rud.)	Intestine
Distomum inerme Linst.	Intestine
? Distomum roseum Bened.	Intestine
Distomum semiflavum Linst.	Intestine
Tylodelphys petromyzontis Brown	Cerebrospinal fluid
Holostomum pellucidum Schlotth. (nom. nud.)	?
29. *Lampetra planeri* Bloch. Planer's lamprey	
"Neuronaia lampetrae" Gulliver	Brain

In the case of the following fishes a list of their Trematode parasites has already been published in "A List of the Trematode Parasites of British Marine Fishes" (Nicoll 1915, *Parasitology*, VII. 339–78).

1. Morone labrax Linn. [=Labrax lupus]	Bass
2. Mugil chelo Cuv.	Thick-lipped grey mullet
3. Mugil capito Cuv.	Thin-lipped grey mullet
4. Gasterosteus aculeatus Linn.	Three-spined stickleback
5. Salmo salar Linn.	Salmon
6. Salmo trutta Linn.	Trout
7. Osmerus eperlanus Linn.	Smelt
8. Clupea alosa Linn. [=Alosa vulgaris]	Allis shad
9. Anguilla anguilla Linn.	Eel
10. Acipenser sturio Linn.	Sturgeon
11. Pleuronectes flesus Linn.	Flounder

In the following fishes no Trematode parasites have hitherto been recorded. They are mostly species of *Salvelinus* and *Coregonus* and it will probably be found that their Trematode parasites are identical with or similar to those of *Salvelinus salvelinus* and *Coregonus oxyrrhynchus* respectively.

1. Salvelinus willughbii Günther	Windermere char
2. „ perisii Günther	Torgoch
3. „ lonsdalii Regan	Lonsdale's char
4. „ struanensis Maitland	Struan
5. „ killinensis Günther	Killin char
6. „ mallochi Regan	Malloch's char
7. „ maxillaris Regan	Large-mouthed char

8.	Salvelinus inframundus Regan	Orkney char
9.	,, gracillimus Regan	Shetland char
10.	,, trevelyani Regan	Trevelyan char
11.	,, colii Günther	Cole's char
12.	,, grayi Günther	Gray's char
13.	,, scharffi Regan	Scharff's char
14.	,, fimbriatus Regan	Coomassaharn char
15.	,, obtusus Regan	Blunt-nosed Irish char
16.	Coregonus vandesius Richards	Lochmaben vendace
17.	,, gracilior Regan	Cumberland vendace
18.	,, pollan Thomps.	Lough Neagh pollan
19.	,, altior Regan	Lough Erne pollan
20.	,, elegans Thomps.	Shannon pollan
21.	,, clupeoides Lacep.	Powan
22.	,, stigmaticus Regan	Schelly
23.	,, pennantii Cuv. and Val.	Gwyniad
24.	Petromyzon marinus Linn.	Sea lamprey

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MACULAE COERULEAE AND *PHTHIRUS PUBIS.*

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(With 5 Text-figures.)

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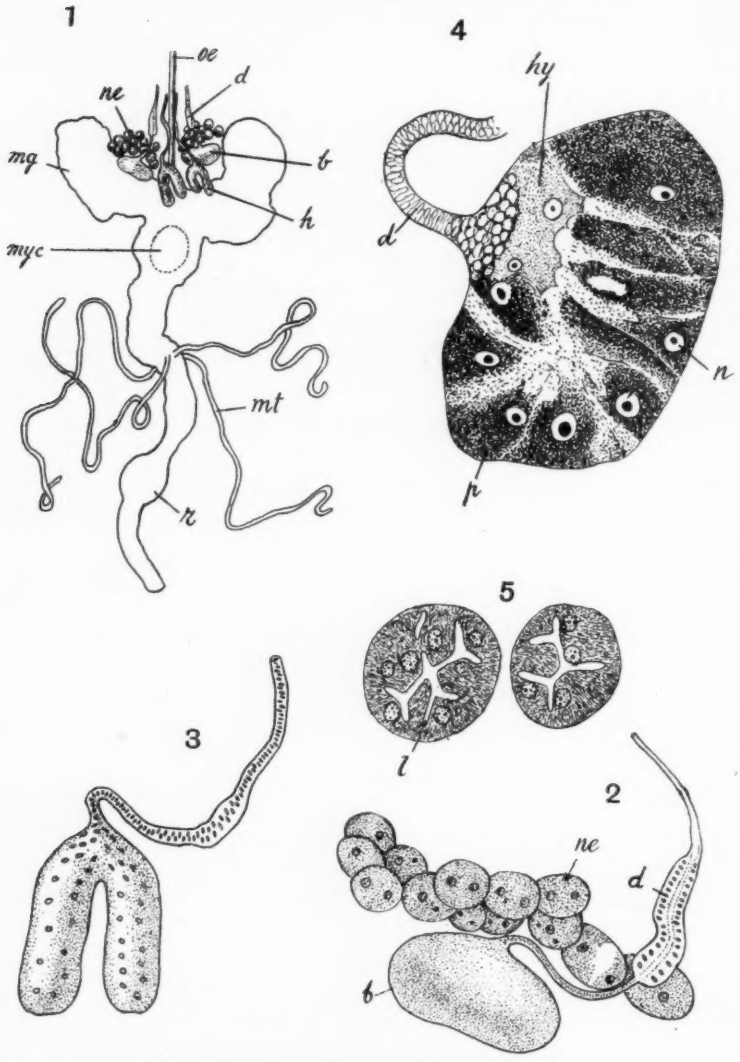
I. Note upon Parts of the Anatomy of Phthirus.

The salivary glands (Fig. 1) consist of two pairs situated between the anteriorly protruding coeca of the midgut. The one pair are bean- or kidney-shaped (*b*) the other horseshoe-shaped (*h*) and extend further backward close to the gut. The four ducts of these glands run forward along the oesophagus, unite, and form a common duct emptying between the dorsal and ventral chitinous stylets of the mouth-parts.

The bean-shaped glands consist of large secretory cells, some ten in number, as seen in longitudinal sections of the gland (Fig. 4). These cells are wedge-shaped and stain so intensely with basophil dyes in respect to their granular protoplasm (*p*) that the latter may obscure the nucleus. This (*n*) is rounded, pale, sharply contoured, with large central chromatin mass. Toward the centre and "hylus" (*hy*) of the gland a part of the secretory cells has a uniform structure and acidophil reaction (secretion?), whilst in the vicinity of the excretory duct the cells are pale and contourless, their nuclei being very pale, and their granular protoplasm staining well with acid dyes.

The horseshoe-shaped glands have a very different structure from the foregoing, a single layer of cells surrounds the central gland-lumen (Fig. 3), the gland, seen in cross-section, showing an irregularly radiate lumen extending between the secretory cells (Fig. 5 *l*). These cells are sharply defined from each other and also on the side of the gland lumen; they appear very pale when stained with acid dyes. The nuclei are vesicular, contain a number of chromatin granules, much linin and nuclear fluid.



Parts of *Phthirus pubis* (drawn by E. Pavlovsky).

Fig. 1. Dissection of alimentary canal and adnexa.
Fig. 2. Beanshaped salivary gland with duct, and adjacent nephrocytes.
Fig. 3. Horseshoe-shaped salivary gland.
Fig. 4. Bean-shaped salivary gland, longitudinal section, Giemsa stain.
Fig. 5. Horseshoe-shaped salivary gland, cross-sections of a branch thereof.

LETTERING TO FIGURES.

b bean-shaped salivary gland; *d* duct; *h* horseshoe-shaped salivary gland; *hy* hylus of gland with acidophil cells; *l* lumen, radial extension; *mt* Malpighian tube; *mg* midgut; *myc* mycetoma; *n* nucleus; *ne* nephrocytes; *oe* oesophagus; *p* protoplasm (granular) of gland cells; *r* hindgut.

The Peri-oesophageal Nephrocytes[1] in *Phthirus* occur in two groups which are situated close to the bean-shaped salivary glands together with which they usually come away (Fig. 2 *ne*) when the glands are removed by dissection.

II. The Experimental Production of Blue Spots by Injection of Emulsions of Bean-Shaped Salivary Glands of *Phthirus*.

The earlier literature on *Maculae coeruleae* in man having been adequately summarised by Nuttall (IV. 1918, p. 375) we would refer the reader to this author for particulars. It is unnecessary to dwell here on the errors of many older authors who misinterpreted the significance of these maculae. It is fully established that the spots are due to the bite of the adult crab-louse. Nuttall (*ibid.* p. 381) writes, however, that "The nature of the maculae remains to be determined, they may be due to extravasated and altered blood." We have sought to solve the problem by experiments herein recorded.

Method: We dissected the living adult *Phthirus* in normal salt-solution under a Zeiss binocular microscope and isolated their various organs in a number of watch glasses where they were triturated in saline until they formed a uniformly clouded fluid. This fluid was subsequently injected into the papillary layer of the skin of men. Precautions were taken to render the manipulations as aseptic as possible. The emulsions were as a rule prepared on the day after the organs had been isolated, these in the meantime being kept in the cold. Such emulsions gave similar results to those freshly prepared.

Our object in using emulsions made from *carefully isolated organs* of *Phthirus* was to determine in which of these organs the active principle occurs which gives rise to maculae, previous authors having experimented with emulsions of mixed organs.

Results: Negative results were obtained with emulsions of (*a*) *midgut*, extending down to union with Malpighian tubes, (*b*) *Malpighian tubes + hind-gut*[2], and (*c*) *fat-body*.

1. *Positive results* were obtained with emulsions of salivary glands as follows:

Experiments with emulsion of mixed bean- and horseshoe-shaped glands.

(*a*) The glands of 4 lice, emulsified in 0·5 c.c. of distilled water and injected into the skin of a man had produced after 24 hours an unusually large blue spot (*ca.* 10 cm. across).

(*b*) The glands of 8 lice were separately emulsified, each set in 1–2 drops of saline. Eight typical blue spots had developed within 24 hours at as many points of inoculation in man.

(*c*) The glands of 10 lice were emulsified together in 10 drops of saline and the dose divided for injection into the skin of the arm of two physicians. Blue spots appeared in both cases at the points of inoculation after the lapse of the usual period.

[1] The true nature of these cells was discovered by Nuttall and Keilin (VI. 1921, pp. 184–192, *q.v.*) working with *Pediculus humanus*; Sikora (1916, pp. 57–58) regarded them as glandular. Graber (1872, p. 137, Pl. XI, Fig. 9 *f.*) took them for uni-cellular gland-cells in *Phthirus*.

[2] Two inoculations on a man's back caused slight inflammatory reaction attributable to uric acid salts in Malpighian tubes.

(*d*) Similar emulsions injected into the shaved skin of a white-skinned dog gave a negative result.

The experimentally induced spots behaved like those produced under natural conditions by the bites of *Phthirus*. After successive changes of colour (bleu, ardoise, ombrée, as described by French authors), the spots disappeared after about the same lapse of time.

To determine which of the two kinds of salivary glands contained the principle capable of causing blue spots, the bean-shaped and horseshoe-shaped glands were carefully separated and used for comparative experiments.

2. *Positive results with emulsions of bean-shaped salivary glands.*

(*a*) Two bean-shaped glands, emulsified in 2 drops of saline, were injected in two places on the breast.

(*b*) Six bean-shaped glands, emulsified in 2 drops of saline, were injected in two places on the back.

(*c*) Eight bean-shaped glands, emulsified in 2 drops of saline were injected.

In all cases blue spots appeared at the points of injection after 24 hours. The spots produced by gland emulsions derived from ♂ lice were slightly paler than when glands from ♀ lice were injected.

(*d*) Eight bean-shaped glands, freed carefully of nephrocytes, emulsified and injected in two places, gave a like result.

3. *Negative results with emulsions of horseshoe-shaped salivary glands.*

(*a*) Eight glands injected as under (*c*) above. Result negative.

4. *Experiments with nutrient agar + fresh human blood.*

(*a*) Fresh blood was added to molten agar in the usual way and poured into Petri dishes. An emulsion of 12 bean-shaped glands in 3 drops of saline was injected into the solidified medium which was afterwards maintained at blood temperature. On the following day a violet discoloration about the seat of inoculation, and measuring 0·5 cm. across, was discernible.

When blood was poured on agar and drops of similar emulsion were applied to the blood with a glass rod, no such discoloration followed at the seat of inoculation.

(*b*) Sixteen emulsified bean-shaped glands in 3 drops of saline were injected into fresh blood agar as under (*a*). Discoloured spots appeared after 24 hours only where the injection had penetrated deeply into the medium.

From these experiments we conclude that the discoloration of blood *in vitro* is analogous to that *in vivo*, the time required for the colour changes to take place being the same in both cases. The absence of oxygen appears essential for the occurrence of the reaction. We obtained the reaction in laked blood after 24 hours at 35–37° C., the fluid having become dark violet in colour. Therefore blue spots in man caused by *Phthirus* are due to affected haemoglobin. A similar experiment with gland emulsion upon agar with tyrosin showed that this substance is not affected by gland emulsion as it is by tirosinase.

5. *Experiment which indicates that the blue spots are caused by a ferment present in the bean-shaped salivary glands.*

Four sets of mixed salivary glands were emulsified and exposed to a temperature of 100° C., drying of the emulsion being prevented. After boiling, the injected emulsion did not produce a blue spot.

We conclude therefore that the active substance is a ferment. Moreover, tests conducted at temperatures ranging from 7 to 52° C. showed that the ferment only produced discoloration in blood-agar at 30–40° C.

Apart from an observation made by Andry, that the skin areas above the blue spots caused by *Phthirus* do not exhibit the phenomenon of goose-flesh as does the surrounding healthy skin, we have no knowledge of the physiological effects of this louse's saliva. We have been able to confirm this observation of Andry's by making casts of the skin surface over and about the areas exhibiting the blue spots induced either (*a*) naturally or (*b*) experimentally, the cold plaster of Paris being moulded upon the skin in cold weather. The casts we obtained show sharply defined smooth areas of skin over the sites of blue spots, the surrounding skin exhibiting very distinct goose-flesh.

III. CONCLUSIONS.

The blue spots induced by the bites of *Phthirus pubis* in man's skin are due to the action of a ferment emanating from the bean-shaped salivary glands of the insects. This ferment acts apparently upon the haemoglobin which, becoming discoloured, causes diffuse bluish coloration of the skin to appear in situations where the insect injects its saliva. We were unable to discover any histological changes in sections of skin showing blue spots[1] and carefully prepared by the acetone method, this negative result conforming with what has been observed in skin affected by jaundice. In contrast to what is seen with normal skin, goose-flesh does not follow upon the application of cold to blue spot areas.

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NOTE: Further references will be found in Nuttall's bibliography (*v. supra*), those above cited not being contained therein.

[1] Confirming Monneret (1868) and Moursou (1877).

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ON THE LIFE HISTORY OF *ANTHOMYIA PROCELLARIS* ROND. AND *A. PLUVIALIS* L. INHABITING THE NESTS OF BIRDS.

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(With 12 Text-figures.)

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I. *ANTHOMYIA PLUVIALIS* L. AND *A. PROCELLARIS* ROND.

Anthomyia pluvialis Linn. (1761) is a very common and beautiful fly, widely distributed in the old world, and easily recognisable by having characteristic black spots on the thorax and abdomen.

Since the description of this fly by Linnaeus it has been carefully studied and redescribed many times, by Fabricius (1775), de Geer (1776), Meigen (1835), Zetterstedt (1838) and others, but more recently by Rondani (1866 and 1877) who found that under the specific name of *A. pluvialis* L. three different species were usually confused: one which is the real *pluvialis* of Linnaeus and two others which he described under the names *A. procellaris* Rond. and *A. imbrida* Rond. These two new species differ from *A. pluvialis*, according to Rondani by having different markings on the thorax, scutellum and abdomen.

The view of Rondani was not generally accepted and was even strongly opposed by Meade (1882) who in his list of British Anthomyidae writes of *A. pluvialis*: "...this common pretty spotted fly varies a good deal, the spots often coalescing so as to alter the design on the thorax and abdomen. Two of the varieties thus produced have been exalted by Rondani into distinct species, but they possess no real specific distinction."

Stein (1907) in his Catalogue of Palaearctic Flies refers to the species *A. procellaris* Rond. and *A. imbrida* Rond. as mere varieties of *A. pluvialis* Lin. In 1906, however, in his paper on European Anthomyids, Stein partly accepts the view of Rondani by admitting the existence of *A. procellaris* as a species distinct from *A. pluvialis*. In this paper he also gives the following three distinctive characters of these two species: (1) the eyes of the male in *procellaris* are placed very close to each other, leaving between them only a very narrow strip of front, while in *pluvialis* the strip separating the eyes is quite distinct; (2) the two posterior lateral thoracic spots in *procellaris* touch the base of the wings while in *pluvialis* they do not reach the wing insertions; (3) the scutellum in *pluvialis* is grey with two lateral black bands, in *procellaris* it is black with the tip only of silvery colour. The problem concerning the validity of Rondani's two new species was recently investigated by J. E. Collin, who has kindly informed me that he is able to confirm Rondani's view in considering *A. pluvialis* L., *procellaris* Rond. and *imbrida* Rond. to be three good and distinct species. Moreover Collin succeeded in discovering a series of new distinctive characters separating the two species *pluvialis* and *procellaris* in which we are specially interested. In a letter of the 3rd of October he writes: "...*procellaris* has a more distinctly pubescent arista, stronger acrostical bristles, stronger and more numerous anterodorsal bristles on hind tibiae, while though I have not examined several dissections of male genitalia for limits of variation, from my knowledge of Anthomyid genitalia the small differences to be found in *pluvialis* and *procellaris* are of specific value. There also appears to be a constant difference in the last abdominal sternite of the male (which is considerably modified in these two species and ends in a laminate projection on each side); *pluvialis* has the hairs in two clusters, those near the tooth longer and stronger than those near the base, *procellaris* has a continuous fringe of hairs all of more equal length and strength."

II. LIFE HISTORY OF *ANTHOMYIA PLUVIALIS* AND *PROCELLARIS*.

1. HISTORICAL ACCOUNT.

We have seen that *Anthomyia pluvialis* L. and *A. procellaris* Rond. were not recognised by the majority of entomologists as two distinct species and in most collections both species are mixed under the name of *pluvialis*. Similarly in the literature of the subject authors almost invariably use the name *pluvialis* when referring to this group of flies, evidently believing all to be referable to the one species. Now considering that the flies are very common and have been known for more than 160 years one would expect to find in the literature sufficient information about their mode of life. A careful search however revealed the fact that our knowledge on this subject was almost negligible.

The first and, as we shall presently see, the most important information concerning the mode of life of *A. pluvialis* we owe to Weijenbergh (1874). It

is contained in the few following words: "*Anthomyia pluvialis* Lin. In April vond ik de popjens in oude vogelnesten." [Transl.: "In April I found the pupae in one bird's nest."]

In 1876 Fairmaire addressed the Entomological Society of Paris a note of a few lines in which he relates as follows an observation made by Dr Danthon of Moulins: "Following a severe inflammation of the ear in a patient to whom he had been called, he extracted several larvae and pupae from which emerged some Diptera belonging to the genus *Anthomyia* and closely allied to *Anthomyia pluvialis*. These larvae injured the bottom of the ear cavity and caused terrible suffering to the patient." Although Dr Danthon and Fairmaire do not actually say that this fly was *Anthomyia pluvialis*, subsequent authors on ear-myiasis (Francaviglia 1914 and de Stefani 1915) and authors of several books of Medical Entomology and Parasitology mention Danthon's case as actually referring to *A. pluvialis*. In 1914 Blankmeyer refers by mistake to *Anthomyia pluvialis* a case of intestinal myiasis, which he had observed. His description and figure of the larva show however that he was not dealing with this genus but with a common species of *Homalomyia*.

We must finally refer to a short note published by Nurse (1914) on *Anthomyia procellaris* Rond. This note runs as follows: "In either May or June 1912 I noticed that the young pears on a tree in my orchard were much infected by Dipterous larvae. Therefore I gathered two or three of the affected pears, in order to ascertain if possible, what insect caused the damage, and placed them in a breeding jar. The pears eventually became mouldy and most of the larvae perished, but I succeeded in breeding at about the beginning of July two or three specimens of the above Anthomyid."

Unfortunately the author does not give more details about the larvae found in his pears nor about the conditions in his breeding jar. It is somewhat doubtful whether the larvae discovered by him belonged to the genus *Anthomyia* and it is possible that the adults of *Anthomyia procellaris* discovered in his jar, if the identification was correct, were either accidently introduced as pupae or penetrated into the jar as adults. We see now, that the scanty information concerning the habitat of *A. pluvialis* and *A. procellaris* when carefully examined may be reduced to the few words of Weijenbergh, who recorded the pupae of this fly in a bird's nest. Weijenbergh's statement has been corroborated by J. E. Collin who (3. x. 1923) informs me that he has bred *A. pluvialis*, *A. procellaris* and two other Anthomyid flies from various birds' nests.

2. Personal Observations.

The larvae of *A. procellaris* and very probably those of *A. pluvialis* were found by me in the nests of birds collected at Tonbridge and kindly sent to me by Mrs A. F. Buxton and Dr P. A. Buxton.

The following is a list of the nests examined and the insects found in them with the remarks of the senders:

NESTS OF	INSECTS FOUND	REMARKS
Parus ater L. (Cole Tit)	Fleas and moth larvae and pupae	The young flew about the 14th June; nest received about 25th June
Parus coeruleus (Blue Tit)	Fleas, adults and larvae	Young flew 13. vi. Nest received 25. vi.
,, ,,	Fleas and *Anthomyia procellaris* L. larvae	10 young flew 10. vi. Received 26. vi.
,, ,,	Larvae of *Mydeae pertusa*, *Appiochaeta rufipes*, *Homalomyia* sp.	Eggs laid, partly incubated and deserted about 4. vi.; nest very wet. Received 27. vi.
Acredula caudata (Long-tailed Tit)	Larvae of *Anthomyia procellaris*, *A. pluvialis*?, *Homalomyia* sp. Staphylinid, fleas	No information, nest received 25. vi.
Fringilla coelebs (Chaffinch)	Larvae of *Anthomyia procellaris*, *A. pluvialis*? and of *Phormia azurea*	No information, nest received 27. vi.
,, ,,	Great number of moth larvae	Young flew 24. vi. Received 28. vi.
,, ,,	Larvae of *Anthomyia pluvialis*?	No information. Nest received about 29. vi.
Pyrrhula europaea (Bullfinch)	No insects	Eggs deserted
Turdus musicus (Song Thrush)	No insects	No information
Hirundo rustica (Swallow)	Larvae of *Phormia azurea*, moth larvae and pupae, fleas	Nest inside which a fly-catcher (*Muscicapa grisola*) laid her eggs and reared four young. The swallows returned and wanted the nest but the fly-catcher kept possession of it. The young were hatched early in July and flew 14. vii. Nest received about 13. viii.
Musicapa grisola (Spotted Fly-catcher	Larvae and pupae of *Phormia azurea*	Nest in open box on Thuya; five young ones, flew 23. vi. Nest received 27. vi.
Acanthis cannabina (Linnet)	Larvae of *Neottiophilum praeustum*	The young flew; nest received 13. vi. composed mainly of hair or wool, nest completely dry
Parus major (Great Tit)	Puparium of undetermined fly	11 eggs laid early in May never hatched, nest deserted

This list shows that of 14 nests, the larvae of *Anthomyia procellaris* and *A. pluvialis*(?) were present in four, in other words about a third of the nests examined harboured these larvae. They were found in one nest of Blue Tit, one of Longtailed Tit, and two of Chaffinch. In the nest the larvae feed on various decomposed organic substances including greasy scales and down left by the birds.

III. SAPROPHAGOUS SPECIFICITY.

In spite of their saprophagous mode of life the larvae of *Anthomyia procellaris* live and are found only in the nests of birds. The numerous investigations of the last 40 years on the fauna of other decomposed organic substances have never revealed in them the presence of these larvae. We are dealing here with a case of saprophagous specificity which is analogous to the specificity of

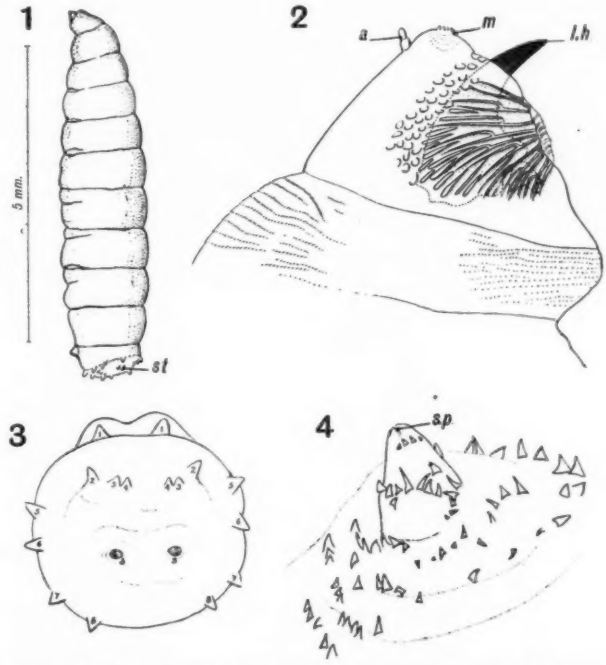
parasites. For the latter it is already well established that they usually occur only in certain definite species of host, while for saprophagous animals the general belief still prevails that they dwell in any decomposed substance. We know however that many of these saprophagous animals, and especially insect larvae, are found only in certain organic substances undergoing a definite stage of decomposition. Moreover, Mégnin (1894) in the course of his study of the fauna of dead bodies, found that necrophagous insects are strictly adapted not only to a definite decomposed body but to definite periods or stages of decomposition. In the present state of our knowledge we cannot go so far as to define chemically the various stages of decomposition attracting the successive fauna of saprophagous animals, but as various animals and plants and their products undergo different processes of decomposition we can at least define the media by the substance which underwent the decomposition. We know now of the existence of a large fauna of coprophagous insects, and the excrement of each group of animals harbours a more or less definite association of these insects. Dead and decomposed snails always contain a special insect fauna and some of the larvae living on them have never been found on other decomposed media. The infected wounds of animals and plants again have their own fauna which is more or less constant and so on. These instances suggest that there is nothing surprising in the case of *Anthomyia procellaris* the larvae of which, in spite of being saprophagous are strictly adapted to a life in birds' nests.

IV. STRUCTURE OF THE LARVA AND PUPA OF *ANTHOMYIA PROCELLARIS*.

The body of the larva is composed of a small pseudocephalon, three thoracic and eight abdominal segments (Fig. 1). The anterior portion of the pseudocephalon (Fig. 2), as in all the cyclorhaphous Dipterous larvae is divided ventrally by a deep groove into two lobes, each bearing a small bell-shaped antenna (*a*) and a slightly raised circular maxillary palp composed of a number of minute sensory papillae (*m*). A series of chitinous ridges arise from the posterior portion of the median groove and spread in a fan-like manner over the ventral side of each lobe. Towards the lateral sides of the lobes these ridges bifurcate, gradually become isolated and pass into scale-like projections with slightly dentate posterior borders. All these projections form naturally on the surface of the head a fan-like system of more or less deep grooves all converging towards the buccal opening which lies in the posterior corner of the large median groove. A wide band, composed of numerous rows of very small hooklets, lies just behind the pseudocephalon. In places the hooklets of the same row lie so closely to each other that they seem to form small transverse ridges with undulated or free dentated ridges.

The anterior portion of each of the eleven segments of the body is surrounded by several rows of hooks pointing backwards. These hooks are very small on the anterior segment but towards the middle of the body they gradually increase in size. In addition to these hooks the posterior portion

of each of the abdominal segments is also surrounded by a series of hooklets pointing forward. There is only one row of these hooklets in the first abdominal segment but the number increases in the following segments and reaches five to six rows in the 6th or 7th segment. The last or 8th abdominal segment differs from all the others by bearing the *anus*, the postabdominal pair of *spiracles* and the sensory papillae (Fig. 3). Its posterior end is truncated and gives rise to eight pairs of conical processes or papillae, each bearing a small sensory pit. The chitinous hooks which cover almost the whole surface of this segment

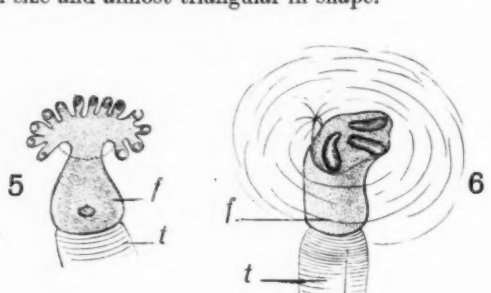


Anthomyia procellaris Rond. Fig. 1. Larva seen from the left side: *st.*, postabdominal spiracles. Fig. 2. Head of pseudocephalon of the larva, side view: *a.*, antenna; *l.h.*, lateral hooks; *m.*, maxillary palp. ×95. Fig. 3. Last abdominal segment seen posteriorly, showing spiracular plates (*s.*) and 8 pairs of papillae. ×35. Fig. 4. One of these papillae showing sensory pit (*s.p.*). ×160.

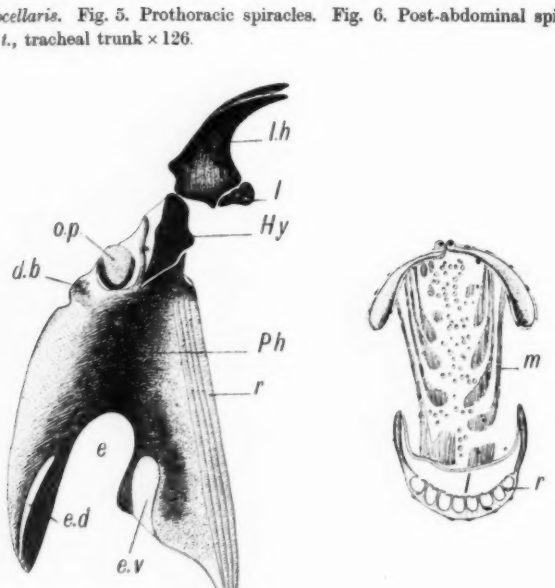
form many sinuous concentric rows, surrounding the anus, spiracles and each of the 16 fleshy processes partly invading also the surface of the latter (Fig. 4).

The larva is amphipneustic, *i.e.* provided with two pairs of functional spiracles: (1) prothoracic and (2) postabdominal. The prothoracic spiracles (Fig. 5) are composed of a short felt-chamber terminating in 13 finger-like processes, each bearing a small circular spiracular papilla. The postabdominal spiracles (Fig. 6) are also composed of a short felt-chamber ending in three elongated papillae converging towards an eccentrically situated external scar,

characteristic of cyclorhaphagous Dipterous larvae. The spiracular plate is rather small in size and almost triangular in shape.



Anthomyia procellaris. Fig. 5. Prothoracic spiracles. Fig. 6. Post-abdominal spiracle: *f.*, felt-chamber; *t.*, tracheal trunk × 126.



Anthomyia procellaris. Fig. 7. Buccopharyngeal armature of the full grown larva: *d.b.*, dorsal band; *e.*, main lateral emargination; *e.d.*, dorsal and *e.v.*, ventral emarginations; *Hy.*, intermediate or hypopharyngeal portion; *l.*, chitinous arc (remains of labium); *l.h.*, lateral hooks; *o.p.*, oval plate; *Ph.*, pharyngeal or basal portion; *r.*, longitudinal ridges—characteristic of saprophagous mode of life. ×65. Fig. 8. Transverse section of the pharynx of the larva: *l.*, lumen; *m.*, dilatory muscles; *r.*, pharyngeal ridges.

The buccopharyngeal armature (Fig. 7) is composed of three distinct articulated portions: (1) lateral hooks, (2) intermediate or hypopharyngeal and (3) basal or pharyngeal sclerites. The two lateral hooks (*l.h.*) are well developed and connected ventrally at their base by means of an arc-like chitinous structure which we have previously described as the chitinous arc (1917) and which probably constitutes the remnant of the labium. The intermediate or hypopharyngeal sclerite (*Hy.*) is very stout and seen ventrally has the shape of the letter H, so characteristic for many cyclorhaphous Dipterous larvae. The basal or pharyngeal portion (*Ph.*), seen from the side shows a wide main lateral emargination (*e.*) and on either side of it, two small (dorsal and ventral) emarginations or clear areas, surrounded by a dark and thickened structure (*ed.* and *ev.*). The two lateral plates of the pharyngeal sclerite are connected dorsally by a very thin membrane which is thickened anteriorly and forms two independent chitinous structures, the one forming a perforated chitinous bridge (*d.b.*) while the other forms two lateral oval chitinous plates (*o.p.*) with thickened borders, each attached to the corresponding side of the basal sclerite. There is a deep notch at the anterior end of the pharyngeal sclerite, within which the intermediate or hypopharyngeal sclerite articulates. Along the dorsal margin of this notch there is a short slightly sinuous rod.

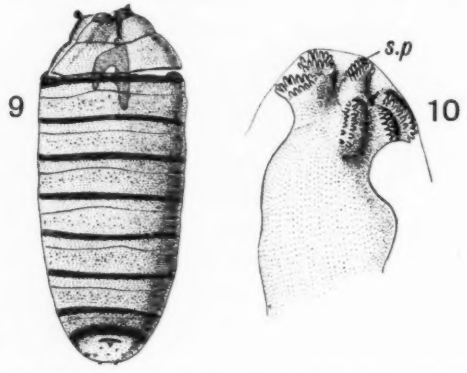
The ventral surface of the pharyngeal sclerite (Fig. 8) is provided with seven T-shaped longitudinal ridges (*r.*) protruding into the lumen (*l.*) of the pharynx and separating the ventral portion of the latter into eight long ductules which communicate with the rest of the pharynx by means of eight long and narrow slits. This structure which is specially seen in the transverse section (Fig. 8) is, as we have previously shown (1915, 1923), a common character of all cyclorhaphous Dipterous larvae which feed on decomposed animals or vegetable substances, in other words which are saprophagous.

The puparium is 4·5 mm. long and 1·8 mm. in diameter; it is of brown colour showing in addition a darker band on each of the abdominal segments (Fig. 9). The cephalopharyngeal armature of the larvae is seen pressed sideways laterally to the ventral side of the puparium. The prothoracic spiracles (Fig. 10) of the pupa are reduced to a felt-tube terminating in six double rows of small papillae. There are no prothoracic horns protruding through the walls of the puparium.

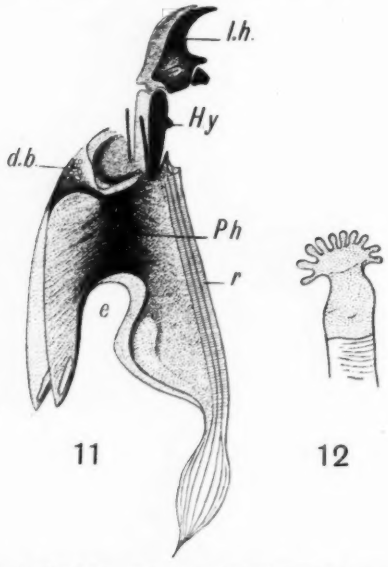
V. *ANTHOMYIA* SPECIES PROBABLY *A. PLUVIALIS*.

The nest of a Long-tailed Tit (*Acredula caudata*) and two nests of a Chaffinch (*Fringilla coelebs*), in addition to the larvae of *Anthomyia procellaris* L., contained a few larvae very similar to them but showing some distinctive characters. Unfortunately these larvae could not be bred through to the adult stage. It is almost certain, however, that they belong to *A. pluvialis* which is closely allied to *A. procellaris*, and is found, according to Stein and Collin, together with the latter species. Considering the great resemblance between the two species, we need mention here only the few following characters by

which the larvae of *A. pluvialis* (?) can be differentiated from those of *A. procellaris*: (1) The body of this undetermined larva, its hooks and post-abdominal papillae and even its cephalopharyngeal armature and spiracular plates are all



Anthomyia procellaris. Fig. 9. Puparium after emergence of the fly. ×12. Fig. 10. Prothoracic spiracles of the pupa, showing spiracular papillae—*s.p.* ×214.



Anthomyia sp., probably *A. pluvialis.* Fig. 11. Buccopharyngeal armature of the full-grown larva, letters as in Fig. 7. ×65. Fig. 12. Prothoracic spiracles of the larva. ×126.

smaller than those of *A. procellaris*. This character is not however very reliable as it is known that the size of various parts in insects may vary to some extent with the relative abundance of food and it is possible that our larvae have been underfed.

(2) The number of papillae in the prothoracic spiracles (Fig. 12) is 10 or 11 instead of 13, as it is the case in *A. procellaris*.

(3) The cephalopharyngeal armature (Fig. 11) is smaller and its dorsal and ventral emargination are less conspicuous; the perforated dorsal band, however, is more developed and the hypopharyngeal sclerite more slender than in *A. procellaris*. The hypopharyngeal portion of this larva has a more characteristic H-shaped structure with long posterior roots.

VI. SOME OTHER FLIES BRED FROM BIRDS' NESTS.

In a recent paper on non-Pupiparous Diptera connected with Birds, Bezzi (1922) gave a complete bibliography concerning this subject. To the references he gives and those cited in my study on *Neottiophilum* (1923) I may add a short note by Scott (1907) on *Mycetaulus bipunctatus*. Scott found three larvae of this Sepsid amongst hairs of an old bird's nest collected on the 17th March, 1907, on the Gog Magog Hills near Cambridge. The larvae pupated late in April and between the 10th and the 13th May flies emerged.

Finally Mr J. E. Collin kindly informs me that in addition to *A. pluvialis* and *procellaris* he has bred from birds' nests two other Anthomyidae namely: *Lasiomma eriophthalma* and what is probably *L. meadei*.

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A NEW GENUS OF TRICHOSTRONGYLID WORMS FROM THE KANGAROO.

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(With 5 Text-figures.)

In the upper part of the small intestine of a Bennett's kangaroo, *Macropus bennetti*, there was found many parasitic worms which, although closely related to *Nematodirus*, differ from members of this genus sufficiently to warrant separation into a distinct genus.

The worms were mostly found about 10 or 12 inches behind the stomach, attached to the intestinal mucosa. They are blood-red in colour, and very small and delicate. As soon as removed to water they roll up into very close spiral coils, as do many other Trichostrongylid worms. They are evidently of Australian origin, since the host was shipped from Australia not more than six weeks before its death in Houston. Only a few days after its arrival in New York it was shipped to Houston, where it died, probably from improper feeding, within about one week.

The parasite is a member of the family Trichostrongylidae Railliet, 1915, and sub-family Trichostrongylinae Leiper, 1908. Whilst resembling *Nematodirus*, it obviously represents a new genus; the name *Austrostrongylus macropodis* is proposed for the parasite.

Austrostrongylus, new genus.

Body slender, of nearly uniform diameter throughout greater part of length, red in colour. Cuticle marked by longitudinal flattened ridges which are provided with a very distinct cross striation; cuticle smooth between the ridges; cuticle of head inflated, the longitudinal ridges not continued on the inflated part. Buccal cavity conspicuous for a Trichostrongylid, with lateral chitinous supports, a relatively large and conspicuous dorsal tooth, and with a smaller perforated ventral tooth. Oesophagus 350μ to 500μ in length. Bursa with a large dorsal lobe and two asymmetrical lateral lobes, the right one larger, with larger rays, than the left, toward which the body curves. Dorsal lobe separated only by slight indentations. Dorsal ray single, deeply bifurcated, and giving rise to a pair of well-developed lateral branches; externo-dorsals long and slender reaching margin of bursa on smaller lobe, but not on larger lobe. Externo-lateral and medio-lateral rays on smaller left lobe moderate in size, approximately equal, associated proximally and separating distally. On larger

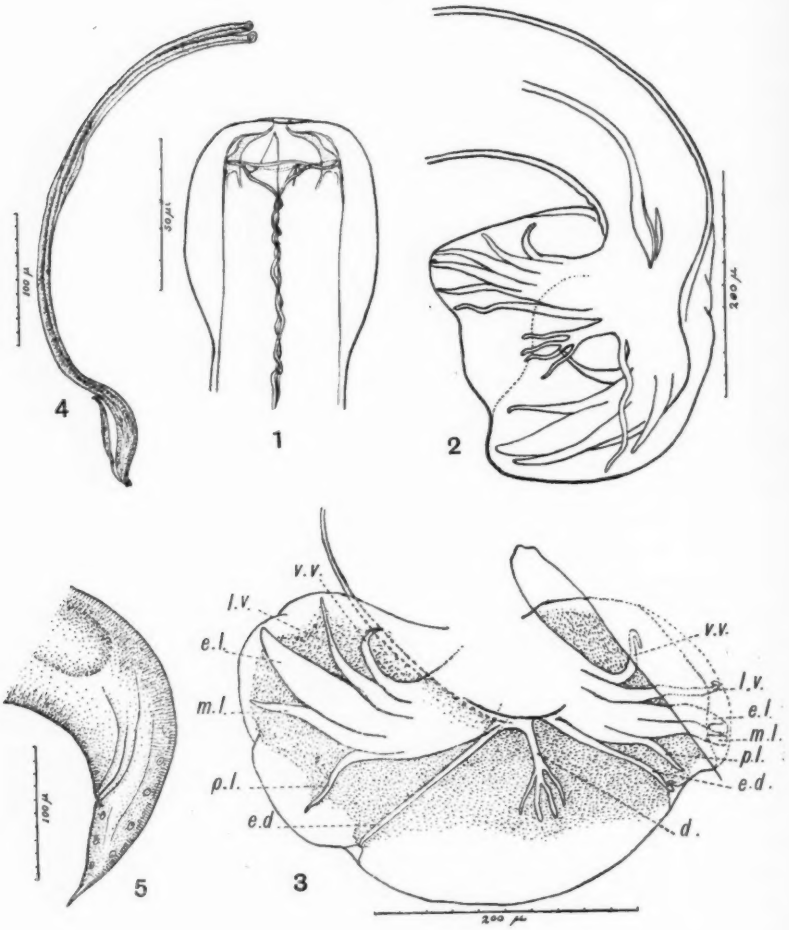
right lobe medio-lateral much larger than externo-lateral, in fact very much larger and thicker than any of the other rays. Latero-ventral rays moderate, associated with lateral rays proximally but diverging from them and curving forward distally. Ventro-ventrals relatively short, tapering, and curved forward away from other rays. Spicules slender, tubular, with a thickened lip at the proximal end, a slight flare near the middle of their length, and with tips curved and flattened like a spoon; the spicules seem to be united by a delicate membrane from approximately the region of the middle flare to the tip. A slender canoe-shaped gubernaculum is also present. Testis simple, not coiled. Vulva in posterior fourth of body; ovijectors well developed. Tail of female tapering abruptly to a fine point. Eggs of moderate size, thin shelled, in early morula stage when deposited. Parasitic in duodenum of kangaroo.

Austrostrongylus macropodis, new species.

SPECIFIC DIAGNOSIS. *Austrostrongylus*. Body very small and slender, blood-red in colour, the females somewhat larger than the males. Cuticle with six or eight longitudinal flattened striated ridges of unequal width, the different ridges in a single individual varying from 10μ to 30μ in width; rest of body smooth, except caudal region of female, which is delicately striated. Cuticle of head inflated as in *Nematodirus*, the inflated region being, however, devoid of striations. Buccal cavity with well-developed chitinous supports, a conspicuous dorsal tooth about 20μ in length, and a small perforated ventral tooth.

Male 4·5 to 5 mm. in length, with a diameter of 126μ to 140μ. Oesophagus 365μ to 390μ in length, the nerve ring near the middle of its length. *Bursa* consists of a large dorsal and two lateral lobes separated only by slight indentations. Dorsal ray single, well developed, with a deep bifurcation at its tip and with two long lateral branches given off a short distance proximal to the bifurcation. Externo-dorsal long and slender, reaching margin of bursa. Smaller left lobe of bursa with three lateral rays nearly equal, moderate in size, the medio-lateral a little nearer to the postero-lateral than to the externo-lateral. Larger right lobe with lateral and ventral rays all arising from a large common trunk, like fingers from a hand. Externo-lateral ray very large and thick, quite out of proportion to all the other rays. Postero-lateral ray small, medio-lateral of moderate size. Spicules 375μ to 500μ long, apparently united by a membrane for the distal three-fifths of their length; gubernaculum small, canoe-shaped.

Female 6·4 to 9·5 mm. in length, with a maximum diameter of 135μ to 175μ; tip of tail abruptly tapered to a fine spine-like point, the anus 85μ to 95μ from tip of tail. Vulva situated from 0·90 to 1·55 mm., or from 1/6 to 1/7 body-length, from posterior end. Ovijectors well developed but short, their combined length about 200μ to 250μ. Eggs lie in uteri in a single row, the young eggs lying with their long axes at right angles to the long axis of the uterus. Eggs 85μ to 98μ by 50μ to 56μ, in about 16-cell stage when deposited.



Austrostrongylus macropodis n.g., n.sp.

Fig. 1. Head of ♀, showing chitinous support of buccal cavity, large dorsal tooth, small perforated ventral tooth, and inflated cuticle.

Fig. 2. Bursa, dorsal view, showing asymmetrical lobes and rays, tip of spicules, and gubernaculum.

Fig. 3. Expanded bursa, ventral aspect, showing form and arrangement of rays. Lettering designating bursal rays: *d.* dorsal; *e.d.* externo-dorsal; *e.l.* externo-lateral; *l.v.* latero-ventral; *m.l.* medio-lateral; *p.l.* postero-lateral; *v.v.* ventro-ventral.

Fig. 4. Spicules and gubernaculum, lateral view.

Fig. 5. Caudal end of ♀, showing tapering tail and spine-like termination.

This parasite, the first Trichostrongylid worm described from Australian marsupials, so far as the writer is aware, is interesting in that it shows a remarkable number of features in common with the genus *Nematodirus*, and yet differs in a number of important respects. As in *Nematodirus* there is a tooth at the anterior end of the oesophagus, but in the Australian worm the tooth is differently arranged, and there is a much more highly developed buccal cavity. As in *Nematodirus* the cuticle of the head is inflated, but in *Nematodirus* it is distinctly striated while in *Austrostrongylus* it is smooth. As in *Nematodirus* the body is marked by longitudinal ridges, but in *Austrostrongylus* these ridges are fewer in number, broad, and marked by conspicuous striations. The spicules are of the same general form as in *Nematodirus*, but there is a small gubernaculum present also. As in *Nematodirus* the body of the female ends in a spine-like process, but in *Austrostrongylus* the tail tapers to the spine instead of ending bluntly.

The most striking feature in which the new worm differs from *Nematodirus* is in the bursa and bursal rays. In these respects it comes much closer to *Graphidium* Railliet and Henry, 1909. The asymmetry of the lateral lobes of the bursa is a very unusual condition, evidently associated with the coiled nature of the body.

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ON THE LIFE HISTORY AND THE ANATOMY OF THE EARLY STAGES OF *FORCIPOMYIA* (DIPTERA, NEMAT., CERATOPOGONINAE)[1].

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(*From the Molteno Institute for Research in Parasitology, University of Cambridge.*)

(With Plates X—XII and 26 Text-figures.)

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[1] Work performed with the aid of a grant from the Medical Research Council.

INTRODUCTION.

DURING the first part of the nineteenth century *Ceratopogon* was the all-embracing genus for a host of blood-sucking and other midges, but toward the end of the century the magnitude of the group and the diversity of the modes of life of its members was realised, and the genus was divided again and again; finally Edwards (1920) decreed that the type, *communis*, was the only species that could rightfully be ascribed to that genus. However, more recently *Psilohelea* has fallen as a synonym of *Ceratopogon*, so the genus has regained some small proportion of its former size. The group is now given the status of a subfamily, Ceratopogoninae (family Chironomidae), and seventeen European genera are recognised by Kieffer (1919). They divide naturally into two groups, those with truly aquatic larvae progressing by means of rapid eel-like wriggling, the adults of which are all bare-winged or with microscopical hairs (*Culicoides*, *Bezzia*), and those whose larvae are terrestrial, living a sluggish life in the exuding sap of trees, under the loose bark of logs, under decaying leaves and manure, in rotting fungi, and in similar forms of decomposing vegetable matter. The wings of the adults of this group are always more or less completely clothed with long hairs (*Forcipomyia*, *Dasyhelea*, *Atrichopogon*). The division of aquatic and terrestrial must not be made too strictly, for exceptions occur in many genera, and we find *Culicoides* normally aquatic but with some species terrestrial (*varius*, *fascipennis*), while *Forcipomyia* exhibits aquatic or semi-aquatic forms.

An explanation is necessary regarding the use of the generic name *Forcipomyia* in view of its confusion with *Ceratopogon* in many papers. The name was first given by Megerlé (in Meigen, 1818) to *albipennis*, but no generic characters were published. Walker (1856) published the name in a key dividing the Ceratopogonines, but still listed all species under the old name *Ceratopogon*. Kieffer (1901) first assigned characters to the genus, which must therefore be attributed to him although he said in a footnote "Je ne puis admettre ce genre." Goetghebuer in 1914 used *Forcipomyia*, in 1920–1 went back to *Ceratopogon*, and in 1923 again used *Forcipomyia*. Edwards is consistent in using the newer name.

The adults of many genera of this subfamily are notoriously difficult to separate, and even the accepted specialists may make mistakes. To my certain knowledge Kieffer has described *Forcipomyia picea* twice, under the names *latipalpis* and *corticicola*, while still recognising *picea* as a distinct species. It is therefore very fortunate that the early stages of most of these difficult groups show such excellent specific characters, and it is remarkable that the larvae and pupae have not been systematically described before. Naturally the early stages of many species of *Forcipomyia* have been described at the time of their discovery, but usually in such a way that the description would fit several species equally well (Dufour (1845), *F. brevipedicellata*, Guérin (1833), *F. geniculata*). Kieffer (1901) made an attempt to compare all the known species

upon an occasion when he had three new ones to describe, and constructed a key for the determination of the larvae based on the nature of the dorsal lanceolate hairs; but this was apparently done with imperfect specimens or from the superficial descriptions of other workers, since some of the characters are not correct. Striking as these dorsal hairs are they are not alone sufficient to separate all species. The most thorough paper on the subject was published by Long (1902) for a number of North American forms, wherein he represented the chaetotaxy to such good purpose that I am enabled to establish the synonymy of his *F. specularis* Coqu. with our *F. brevipennis* Macq., and with less certainty to suggest that his *F. brumalis* Long may be our *F. bipunctata* L. I have made a practice of obtaining Mr F. W. Edwards' confirmation of all my synonyms by means of the adults.

In a subsequent paper a number of exotic larvae of *Forcipomyia* will be discussed, forms similar to Carter's *ingrami* (1919) and others which would justify the establishment of new genera were not the adults so similar to type.

The obvious drawback to the method of classification by immature forms is that these stages are only known in a small proportion of the species recorded. Classification by larvae can therefore never supersede classification by adults, but it will be of great and ever increasing supplementary importance as more and more species are discovered in their larval state. The characters to be relied upon for specific determination have been established by a comparative morphological study of the nine species at my disposal.

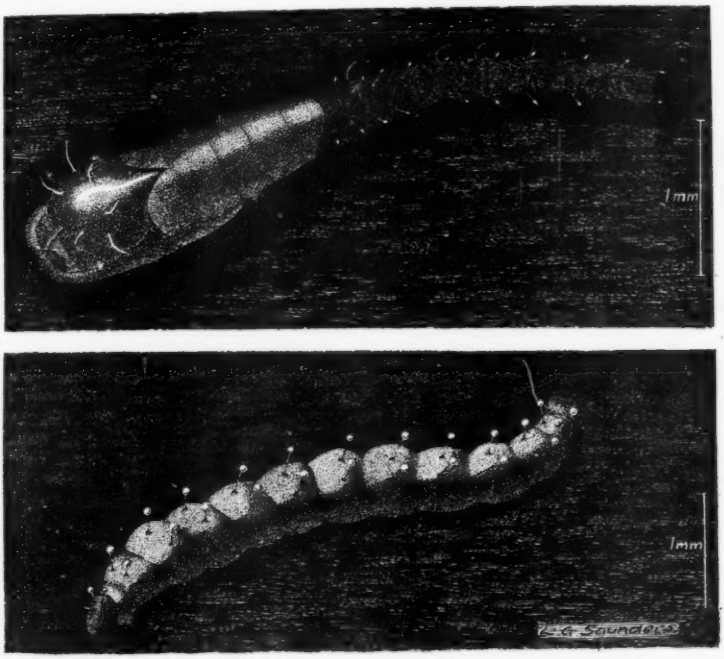
Since some *Forcipomyia* larvae are among the largest of Ceratopogonines, and are available throughout the winter, they constitute excellent subjects for the study of the anatomy and mouth-parts. Nothing has hitherto been published on the internal anatomy of any members of this subfamily, so it has not been discovered before that the malpighian tubules are reduced to two, or in some cases three, the latter condition being unique among insects. The mouth-parts have been only superficially described before (Goetghebuer, 1914), and the marvellously-constructed hypopharynx is here figured and described in full detail for the first time.

HABITS OF LARVAE.

As was mentioned in the introduction, *Forcipomyia* larvae occur in a great variety of places, always closely associated with some form of decomposing vegetable matter. With the exception of *F. pulchrithorax*, a sap-inhabiting form, they are always to be found in some dark enclosed cavity where the atmosphere approaches saturation. This condition favours the growth of moulds and other fungi which serve as food; the decomposing vegetable matter may also be eaten to some extent, but conidial spores and sections of hyphae can always be found in the intestine.

The larvae are gregarious in habit, most species occurring in quite large colonies, 20 to 100 or more. When first exposed their appearance is most striking, for each lanceolate hair in the double row on the back and on the

head bears a minute shining droplet of water (Text-fig. 1). A hygroscopic substance within the bulbous tip of the hair collects moisture from the atmosphere, and it is thought that this water flowing down the pedicel of the hair keeps the skin moist to facilitate cuticular respiration (Keilin, 1918). The winter is passed in the third or fourth larval stage. The location of the winter generation is not always the same as that of the summer ones; for instance *F. radicicola* hibernates in the rotting tap roots of annuals, but the summer generations must find some other food supply, in default of their winter



Text-fig. 1. *F. bipunctata*, larva and pupa *in situ* on rotten wood. Larva showing characteristic droplets of water accumulated by dorsal lanceolate hairs.

quarters. This summer habitat has not yet been discovered, in spite of the most careful search.

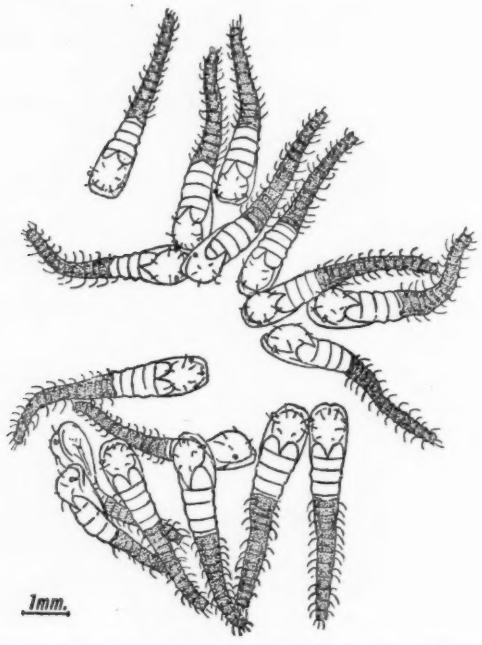
Pupation occurs as soon as warm weather sets in, and the first summer generation is started by the end of May. Thereafter follows a series of generations, three or more in the year; it is impossible to breed these insects in captivity and so follow the number of generations throughout the year on account of the unknown feeding habits of the adults, so the information must be obtained by careful observation in the field. The larvae pass through four stages before pupating, the length of time between moults being about one week, but this depends largely upon the temperature. A detailed account of the early stages

is given for *F. picea* in which species the development has been carefully followed.

PUPATION.

Pupation occurs wherever the larva happens to have been feeding, but the bark-inhabiting species maintain the gregarious instinct, so that groups of pupae will be found with their heads directed towards the centre and their bodies and empty larval skins stretching out behind like the spokes of a wheel (Text-fig. 2).

The members of this genus and its close relative *Atrichopogon* form one of the few groups of Diptera Orthorrapha that retain the larval skin in the pupal



Text-fig. 2. *F. bipunctata.* Group of pupae in natural position, showing gregarious habit.

stage. The known instances of this adaptation are as follows: Stratiomyidae retain the skin over the entire body, like the Cyclorrhapha; Scatopsinae (Bibionidae) emerge sufficiently to free the portion of the thorax bearing the respiratory horns; *Dactylolabis* and *Cylindrotoma* (Tipulids) emerge partially; and *Forcipomyia* retains the skin on the last four or five abdominal segments (Text-fig. 1). Some of the aquatic Chironomids (*Chironomus, Tanypus*) that pupate inside a tube or case do not free themselves from the larval skin until they wriggle out to rise to the surface and emerge, but it does not invest them closely or form any protection or anchorage as in the terrestrial forms.

HABITS OF ADULTS.

Although furnished with well-developed piercing mouth-parts the adults of *Forcipomyia* never attack warm-blooded animals. They will feed readily on any flowers or sweetened material offered them, but the females seem unable to mature their eggs without a meal of blood from their particular host. A number of records exist of the feeding of *Forcipomyia* females on larval and adult Lepidoptera, and on other insects such as *Sialis* and *Meloe*. Edwards (1923) has recently collected all existing records of the feeding of Ceratopogoninae, and appended a complete bibliography; it is noteworthy that all instances have been stumbled upon accidentally. All attempts to furnish the right host to *Forcipomyia* females in captivity have resulted in failure, either because the favourite was not included among those supplied or because the adults would not behave normally in captivity. (*Culicoides varius*, a voracious blood-sucking Ceratopogonine, refuses to bite even when confined upon the thinnest-skinned part of the wrist or hand, and at the normal time for feeding.) It has therefore been impossible to obtain eggs laid in captivity, and all efforts to find the eggs under natural conditions have been unsuccessful.

MORPHOLOGY OF LARVAE AND PUPAE.

The complete external and internal anatomy has been investigated in the larvae of *Forcipomyia bipunctata*, the type species, while the others are briefly described with reference only to their specific characters.

I. *Forcipomyia bipunctata* (Linnaeus) 1767.

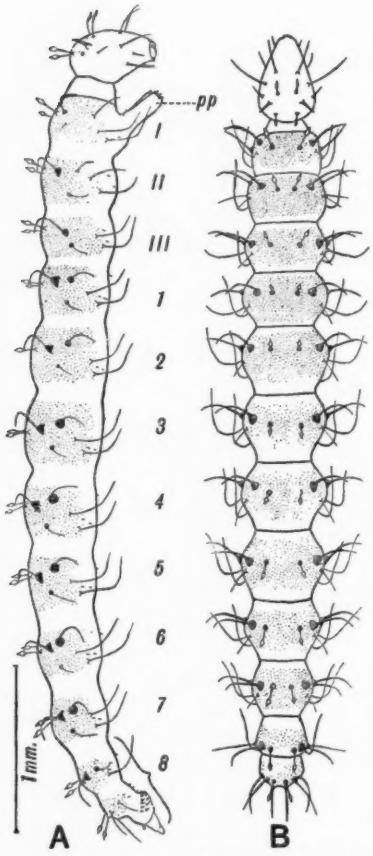
F. trichoptera (Meigen) 1818.

There is no doubt that the species recognised under these names by Edwards and Goetghebuer respectively are synonymous; I have compared the larvae of both and find them identical. Goetghebuer (1923) acknowledges this, but apparently considers *bipunctata* wrongly applied, since he adheres to *trichoptera*. With Mr Edwards' permission I quote a passage from a letter he wrote to me recently explaining his views: "Regarding the name *bipunctata*, there has been some confusion. Linnaeus in his original description says 'thorax laevis,' which I interpret as referring to the shining mesonotum characteristic of Meigen's *trichoptera* (described much later). Zetterstedt, Kieffer, and perhaps others use the name *bipunctata* for another allied species (also common in some parts of England) which has an entirely *dull* mesonotum, but it seems to me that they are wrong in so doing."

There is some reason to suppose that the American species named *brumalis* by Long (1902) is synonymous with *bipunctata*; the adult descriptions are very close, but the incomplete figures of larvae and pupae afford no conclusive evidence. (The most one can say is that they show no characters not belonging to *bipunctata*.) Early descriptions were written by Loew (1843), Walker (1856),

Brauer (1883), and Theobald (1892), but specific characters are difficult to recognise. A fuller account, though still incomplete, has recently appeared by Goetghebuer (1923).

In habitat *F. bipunctata* is less specialised than most species. The anatomical studies were made in the winter of 1921–2 with material from beneath the bark of logs, taken in company with *F. picea*, but it has since devolved that the larvae occur more frequently in other situations. Specimens were found in an old, well-rotted manure heap in the summer of 1922 and again in the spring of 1923, showing that they may hibernate there as well as under bark. Hibernating larvae were also found in rotting waterweed that had been raked from a mill stream at Great Shelford, Cambs. (18. iii. 23).



Text-fig. 3. *F. bipunctata* larva. A, lateral, B, dorsal view. I, II, III thoracic segments; 1–8 abdominal segments; *pp*, prothoracic pseudopod.

(A) LARVA.

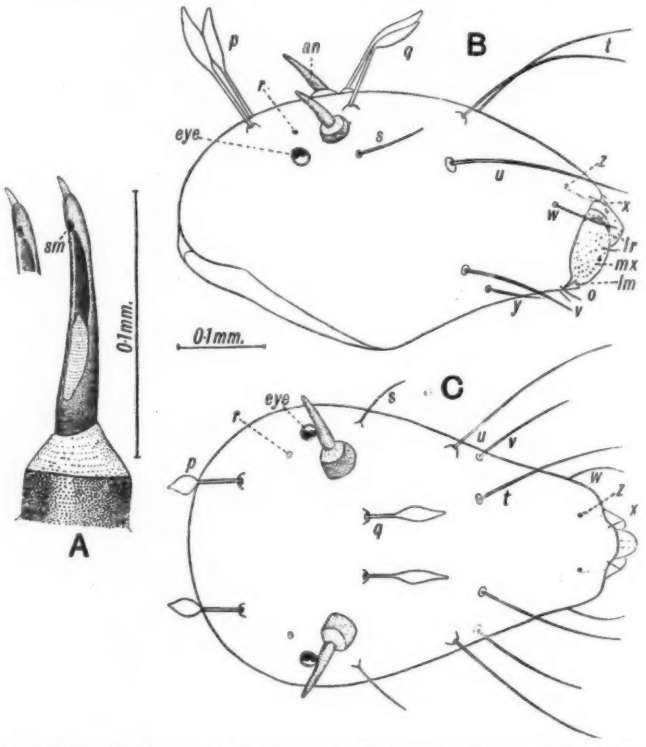
The full-grown larvae are 4·5 mm.–5·0 mm. long, cylindrical, slightly compressed dorso-ventrally, with a well-developed head and distinct body segments. In colour they are whitish, often exhibiting dark markings between the segments where the contents of the alimentary canal show through. The moist condition of the skin, however, causes fungus spores and other material to become caked on the body, and the minute cuticular armature helps to retain this matter in varying degree on all surfaces except the venter which is kept clean by the constant gliding motion of the larvae; thus the natural colour is masked by yellowish or brownish substances.

The larva consists of a head, three thoracic, and eight abdominal segments, the eighth or terminal being divided into two apparent segments.

EXTERNAL ANATOMY.

Head.

The Head is rounded, roughly pyriform, the mouth-parts forming the narrow anterior end, while the occipital foramen is not directly opposite, at the broad posterior end, but slightly ventral, so that the head is joined to the body normally at an angle of about 70°. No individual sclerites are distinguishable in the skull-like capsule of the head, though in many other species the frontal



Text-fig. 4. *F. bipunctata* larva. A, antenna. B, lateral view of head. C, dorsal view of head. *an*, antenna; *lm*, labium; *lr*, labrum; *mx*, maxilla; *o–z*, twelve paired sensory hairs and pits; *sm*, sensorium.

suture may be readily discerned. The colour of the head is yellowish-brown, without markings on the vertex.

The Antennae (Text-fig. 4), 0·13 mm. long, are situated on the dorsal surface of the head rather more than a third of its length from the posterior margin, well apart from the median line. They consist of a short basal portion connected by a membrane to a slender tapering rod which bears at its tip a minute finger-like projection. Near the base on one side of this rod is an elliptical

opening in the chitin with a thin membrane stretched across it, and from its distal margin the antenna is hollowed to form a trough which extends almost to the tip. One, or in some instances two, minute sensory pits occur at the distal extremity of this groove (Text-fig. 4, A, *sm*).

The Eyes (Text-fig. 4) are slightly posterior and laterad to the antennae; their aperture in the chitinous wall of the head is subspherical, smaller than that of the antennae, and is covered by a simple transparent lens, beneath which may be seen the pigment essential to all functional eyes.

Chaetotaxy. Twelve pairs of sensory hairs and pits occur upon the head, excluding the sensory organs on the mouth-parts. They have been given an arbitrary lettering in order that they may be compared with corresponding hairs on the head of other species. There are two pairs of lanceolate hairs (*p* and *q*), seven pairs of ordinary tapering setae, and two pairs of minute sensory pits; the nature and disposition of these structures may readily be seen in Text-fig. 4, B, C.

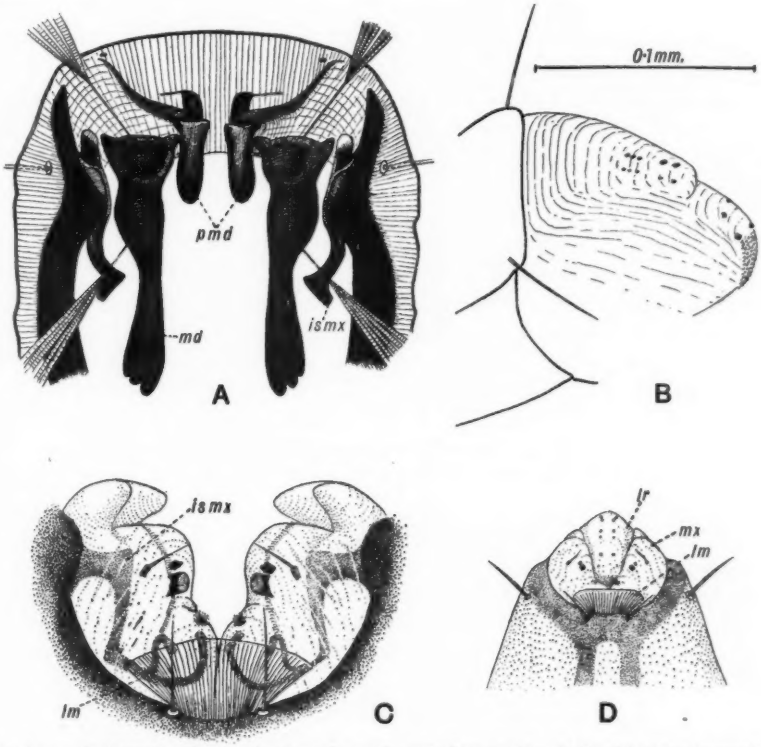
The Mouth-parts. The external structures may be homologised fairly closely with those of related forms, but there is no larva outside the Ceratopogoninae that can show an internal structure comparable with the hypopharynx peculiar to this group.

The mouth-parts consist of a labrum with a pair of small premandibles, a pair of large mandibles, a pair of maxillae, a labium, and an internal hypopharynx. The anterior extremity of the wall of the head is heavily chitinised to form a ring supporting the more delicate mouth-parts.

The Labrum (Text-fig. 4, B and Text-fig. 5, B, D, *lr*). The slightly extended dorsal portion of the head capsule, extending back as far as the sensory pits *z*, must be regarded as part of the labrum since beneath it occur the premandibles; a study of *Chironomus* will show that these organs are unquestionably labral. The greater part of the labrum, however, is a narrow fleshy protuberance with membranous walls, extending forward and downward to recurve within the mouth (Pl. XII). Its front is furnished with paired sensory organs in the form of chitinous rods imbedded in the fleshy substance of the labrum, their distal ends just emerging through the membranous wall; their disposition may be seen in Text-fig. 5, B. On the lower front corner, just at the entrance to the mouth-cavity, there is a small triangular area covered with minute papillae.

The Premandibles. On the sides of the labrum in *Chironomus* there are movable processes which Goetghebuer (1912) named "premandibles" on account of their mandibular appearance and because they occur in front of the mandibles. He does not suggest that they are homologous with the mouth-appendages of *Campodea* known as premandibles (Berlese, 1909), and therefore the term should not have been used; however it is now generally accepted, so I have retained the name in this paper in order to avoid confusion. Goetghebuer advances an hypothesis that these organs are appendages corresponding to a special cephalic segment, and finds in them an argument for

the conception of the labrum as a pair of appendages fused together, like the labium. But there are lobes of the labrum whose membranous walls are continuous with the sides of the premandibles for almost their entire length, and a cross section shows that the chitin is in a single plate, not hollow like a true appendage, so that they must be regarded rather as local thickenings of the labral wall.



Text-fig. 5. *F. bipunctata* larva. A, view of mouth-parts from within the head looking forwards; labrum not represented. B, labrum alone, dorso-lateral view. C, maxilla and labium, front view. D, ventral view of external mouth-parts. *ismx*, internal chitinous support of maxilla; *lm*, labium; *lr*, labrum; *md*, mandible; *mx*, maxilla; *pmd*, premandible.

In *Forcipomyia* the premandibles (Text-fig. 5, A, *pmd*) are a pair of small chitinous rods hinging upon processes which depend from the roof of the labrum; I homologise these processes with Goetghebuer's "pièces triangulaires" in *Chironomus*, the posterior portion of the labrum being very much reduced. At their upper end they are distinctly fused with the walls of the labrum, but in sections their lower extremity appears free within the wall, though doubtless a fold of the membrane encloses them. A strong muscle is attached by a long tendon to the proximal end of the premandibles, and in living larvae under

the microscope they may be seen to move backwards and forwards rapidly in the sagittal plane. They occur so far up under the roof of the labrum that they cannot help in passing the food down into the mouth as is claimed for *Chironomus*, and indeed they are not shaped for such work, but their powerful musculature, and their complexity in *Dasyhelea*[1], point to some important function which I cannot yet determine.

The Mandibles (Text-fig. 5, *md*) are long black structures, heavily chitinised, hollow for the greater part of their length, narrow in the middle, and flattened distally into a spoon-like three-toothed blade. No setae or brush-like groups of hairs occur upon them. They cannot function as biting organs because the labrum separates them, but they work vertically between the labrum and the maxillae, paddle-fashion, scratching up food material and conveying it into the mouth.

The Maxillae (Text-fig. 5, *mx*) when seen from the side are semicircular protrusions with two distinct lobes, all of a similar thin-walled nature to the labrum; they occupy a position on either side of the labrum and extend down to the labium. A curving internal support of chitin arises from the side wall of the head and forks at its extremity as seen in Text-fig. 5, C (*ismx*). The sensory organs of the maxillae consist of a very short cylinder, an indefinable bar, a minute seta articulated with a short basal portion, and a brush-like group of exceedingly small hairs.

The Labium (Text-fig. 5, C, D, *lm*) is a simple chitinous plate projecting from the antero-ventral side of the head; its distal margin is slightly curved and smooth.

The Hypopharynx (Pl. X). This term has always been used to designate the complicated internal structure in the head of Ceratopogonines, and for the sake of convenience it is retained in this paper. It must be recognised, however, that other sclerites are involved in its composition besides the true hypopharynx. The mastication of food is performed by this organ in terrestrial larvae, and it assists in ingestion in those forms subsisting on semi-liquid nutriment. I have watched a *Bezzia* larva under the microscope sucking out the contents of a *Tanypus*, and the hypopharynx worked rhythmically like a pump all the time. From the position of the walls of the buccal cavity it is evident that the whole is an invagination into the pharynx. In some other Chironomids (*Chironomus*, *Pelopia*) there is a hypopharynx in the form of a plate receiving the salivary duct, which bears some resemblance to the ventral portion of the hypopharynx in *Forcipomyia*, but there is nothing to correspond with the portion above the oesophagus. Goetghebuer (1914) described it as a single mass, apparently not having discovered its several component parts. Keilin (1921) succeeded in distinguishing more sclerites in *Dasyhelea*, but the larva is too small for thorough anatomical dissection.

From the base of the labium two lateral rods (*lrs*) run backward and upward, each dividing dorso-ventrally into two and then meeting again,

[1] In *Dasyhelea* each premandible is divided into two.

terminating in a tendon which passes up to the outer surface of the lateral wings of the hypopharynx. Near the middle the divided portions of each rod are connected by a short vertical rod, and another rod is given off above this (*rl*); these are embedded in the sides of the labrum to support it laterally. It is possible that this system of rods is derived from the tentorium, but at present there is no evidence to support such a view.

The hypopharynx itself consists of two principal parts, a dorsal and a ventral, between which the food is ground and passed back into the oesophagus. The dorsal (*dhy*) is composed of a central portion to which are attached two wing-like sclerites (*lw*). The central portion is approximately shaped like a very short, broad boat, being rounded on the bottom, with three transverse ridges to facilitate the grinding of food (Pl. X, fig. 6). It is hollow antero-dorsally (Pl. X, fig. 5), and from the postero-ventral margin two thin triangular plates of chitin curve backward and upward with strong striations running across them; these striae continue into a thin colourless membrane so that they resemble a fringe of hairs, and have hitherto always been regarded as such. The membrane continues beyond the striae and lies loose in the oesophagus, but usually breaks off during dissection.

The lateral wings are articulated with the central portion and with each other upon the middle dorsal projection of the former; they have a strong reinforcing rib running down the centre of the inner surface, and another passing forward and downward from the tip to the anterior corner. They are usually at an angle of about 95° with each other, but may be drawn together by a strong connecting muscle. From the outer surface of the tip of each wing a strong rod (*sr*), attached at either end by a stout tendon, passes down to the ventral portion of the hypopharynx forming a kind of suspensory hinge for the two grinding surfaces.

The ventral portion of the hypopharynx is one single sclerite of an inverted saddle shape (Pl. X, fig. 3); it is studded with small rounded teeth on its grinding surface. A short round rod proceeds forward from each corner of the anterior margin and connects with a small triangular sclerite leaving a space through which the salivary duct opens (Pl. X, fig. 2, *sd*). A thin plate stands up in front of the aperture, serving to keep food from blocking the duct; it may often be seen bent back over the opening. The chitinous intima of the oesophagus, at its junction with the posterior margin of the ventral portion of the apparatus, is striated, presenting the appearance of a fringe of hairs as in the dorsal portion.

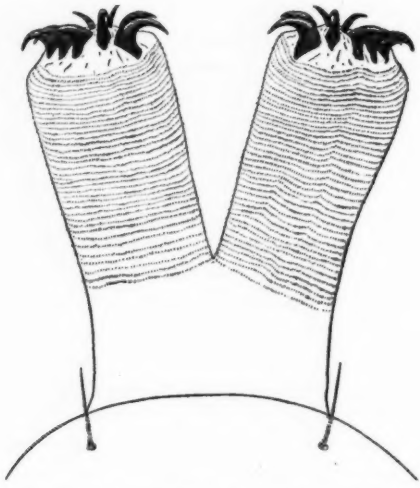
In addition to these parts there is an accessory structure in the form of a bridge (*bg*) between the two lateral rod systems, just in front of the dorsal portion and connected with it by a membrane. It may be seen *in situ* in Pl. X, fig. 1, diagrammatically in Fig. 2 (only the left half shown), and dissected out in Fig. 4. From the upper, chitinous bridge a membrane extends downward and backward into the lumen of the pharynx between the grinding surfaces, its lower edge striated into a fringe as in other parts of the hypo-

pharynx previously described. The membranous wall of the labrum which runs back in the roof of the mouth joins this bridge structure on its anterior surface (*ml*).

The function of the hypopharynx will be discussed under the heading Musculature.

Body.

In the full-grown larva the developed imaginal discs in the thorax give these segments a shorter, broader form than those of the abdomen, otherwise the only distinction is a minute difference in chaetotaxy and the presence of a pseudopod on the prothorax. From the sixth to the last abdominal segment a steady decrease in size occurs, the last half of the eighth bearing a ventral, protruding, hook-studded ridge, scarcely to be called a pseudopod, but functioning as such.

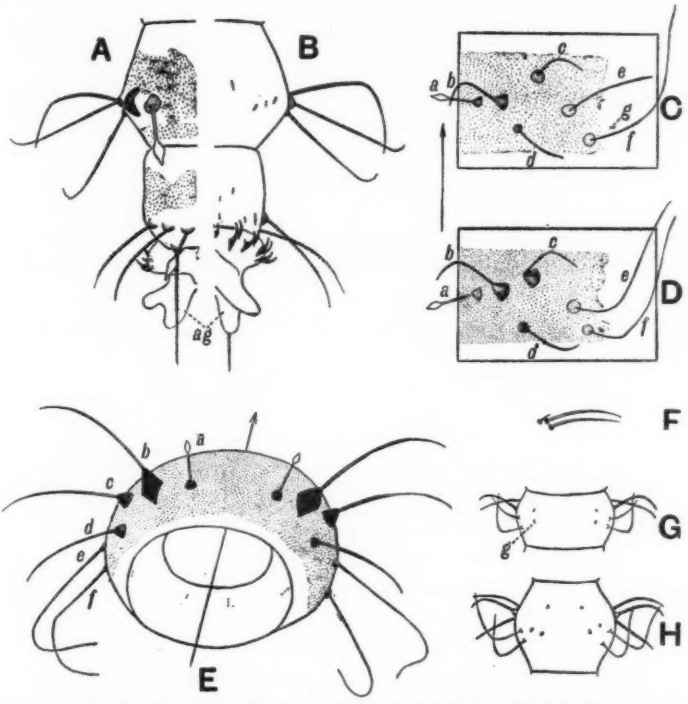


Text-fig. 6. *F. bipunctata* larva. Prothoracic pseudopod.

The Prothoracic Pseudopod (Text-fig. 6) is a retractable fleshy organ with membranous walls, situated ventrally upon the first thoracic segment. It has a short, broad base, and is bifid distally, the apex of each branch being crowned with six strong, black, backward-directed hooks and two weak central ones. From the base of the hooks back to the point of bifurcation the wall of each branch is ringed with microscopical setae.

The Extremity of the Abdomen (Text-fig. 7, A, B). Above the anus, which opens somewhat ventrally, two short, bilobed blood-gills (*ag*) may be extruded, while below and in front a fleshy ring extends across the venter bearing two rows of four hooks each on either side of the median line, and two small hooks in the middle, all being directed backward.

Chaetotaxy (Text-figs. 7, 8). Each segment including the two halves of the last abdominal bears a pair of swollen-tipped, spear-shaped hairs on the dorsum, and five pairs of simple chaetae are regularly disposed on all segments but the eighth abdominal. Of these only the two lower pleural ones (*e*, *f*) are smooth; the others are all more or less setaceous (Text-fig. 8). The integument of the dorsum and half the pleurae is armed with minute hooks (cuticular armature) shown in detail in Text-fig. 8 (*h*) and represented by stippling in

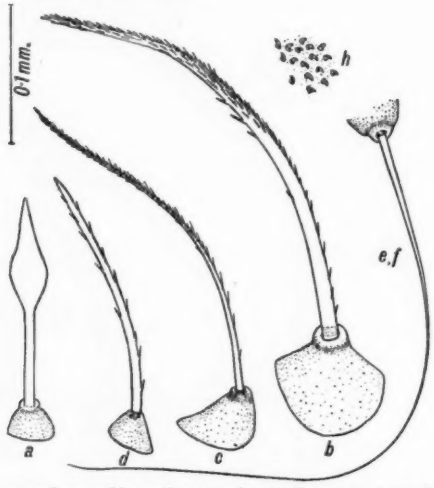


Text-fig. 7. *F. bipunctata* larva. A, dorsal, B, ventral view of eighth abdominal segment. C, setal plan of mesothorax, median dorsal line to median ventral line. D, the same, second abdominal segment. E, perspective drawing of single abdominal segment. F, highly magnified drawing of the group of hairs *g* (rudimentary sense organs of the legs). G, ventral view of mesothorax. H, the same, second abdominal segment. *ag*, anal blood-gills; *a–f*, macrochaetae; *g*, group of microchaetae.

Text-figs. 3, A, B, and 7, A, C, D, E. Ventrally the integument is smooth and polished. On the thoracic segments there is an anterior ventro-lateral pair of microchaetae and behind them a group of three set very close together (*g*), which represent the vestigial sensory organs of the legs (Keilin, 1915) situated at the point of attachment of the imaginal discs of the legs (Text-fig. 7, C, F, G). The abdominal segments each bear three pairs of ventral microchaetae (Text-fig. 7, H). The chaetotaxy of the last abdominal segment differs from that of

the others in that there are only two pairs of macrochaetae on each half in addition to the dorsal *a* hairs (Text-fig. 7, A). The first half bears the normal number of ventral microchaetae, but the second bears five pairs (Text-fig. 7, B).

From the second abdominal segment backward, in the full-grown larva some time previous to pupation, each segment develops a transverse cuticular bar connecting the bases of the *a* hairs.



Text-fig. 8. *F. bipunctata* larva. Macrochaetae of a single segment much enlarged. *h*, dorsal cuticular armature.

Internal Anatomy.

Digestive system.

The digestive system consists of: buccal cavity, hypopharynx, oesophagus, mid-gut, and hind-gut, with the salivary glands and malpighian tubules.

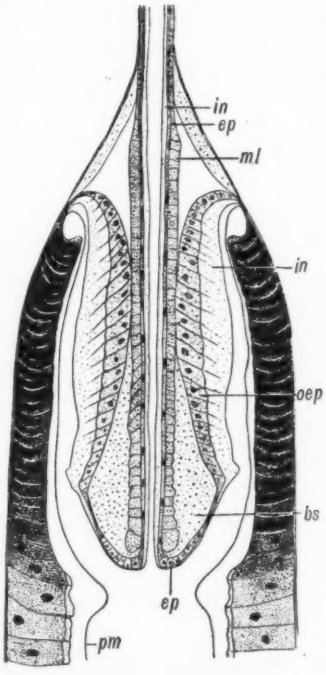
The Buccal Cavity (Pl. XII, *mc*) extends upwards on either side of the reflected labrum, forming chambers in which the mandibles work. The labrum forms the roof, the lateral rod systems the sides, and the dorsal surface of the ventral portion of the hypopharynx the floor of the cavity. The epithelium secreting the chitinous intima of the walls invests the whole hypopharynx and is continuous with the walls of the oesophagus behind.

The Hypopharynx occupies the portion of the fore-gut usually known as the pharynx.

The Oesophagus (Pl. XII, *oes*) is a simple tube leading back to the oesophageal valve at the beginning of the mesothoracic segment. Its muscular and epithelial walls are thin, but it has a very thick chitinous intima folded into longitudinal ridges, which close the lumen except when food is passing down.

The Oesophageal Valve (Text-fig. 9) consists of an extension of the oesophagus into the cavity of the mid-gut, carrying with it all three layers, the muscular, epithelial, and chitinous intima, and folding the two last back upon themselves

with the inclusion of a blood space. The greatly attenuated epithelium of the oesophagus (*ep*) regains its formation of cubical cells at the posterior end of the valve, where it is reflected widely to enclose a blood space (*bs*); the returning later of epithelium develops into large columnar cells of open fibrous cytoplasm with large nuclei (*oep*); anteriorly it is reduced again where it curves back to join the epithelium of the mesenteron. The chitinous intima (*in*) is carried around the entire valve, though it is very thin at the posterior bend; on the reflected surface of large epithelial cells it is secreted in a very thick layer showing slight striations proceeding from the secreting cells. The muscular layer (*ml*) of the oesophagus extends only to the posterior end of the valve, where it forms a band of strong circular muscles capable of closing the lumen to prevent regurgitation. The walls of the portion of the mesenteron enclosing the valve are thin, being composed of strongly staining crescentic cells which straighten and increase in size caudally to become the typical large columnar cells of the mid-gut; thus the portion containing the oesophageal valve may be regarded as a distinct region, the *cardia* of Miall and Hammond (1900) and *proventriculus* of other authors. In Anophelines and Culicines (Imms, 1907) an even simpler refolding of the tissues occurs, but there is included a definite ring of tissue which the author calls the blood sinus, in addition to the blood space between the folds. In *Chironomus* (Miall and Hammond) there is a secondary folding of the epithelium, but very meagre secretion of chitinous intima.



Text-fig. 9. *F. bipunctata* larva, oesophageal valve, longitudinal section. *bs*, blood space; *ep*, epithelium; *in*, chitinous intima; *ml*, muscular layer; *oep*, outer fold of epithelium; *pm*, peritrophic membrane.

The Mesenteron (Pl. XI, *mg*) is a simple cylindrical tube devoid of caecal chambers or accessory structures of any kind. It extends from the mesothorax to the middle of the sixth abdominal segment, and is of uniform diameter throughout except at the sharply tapering extremities. Its wall consists of columnar epithelium with a somewhat broken and irregular striated inner margin (the "ciliate layer," "striated hem," "plateau strié" of other authors) which is prominent in the fore part but subsides and almost disappears towards the end of the mid-gut. The usual peritrophic membrane occurs within the mesenteron enclosing the food.

The Hind-gut (Pl. XI, *hg*) has a thin-walled chamber at its junction with the mesenteron, and the remainder is a small muscular tube capable of doubling back when the larva contracts longitudinally. It joins the rectum with a slight enlargement in the first half of the last abdominal segment.

The Rectum (Pl. XI, *rt*) is larger in diameter but shorter than the hind-gut; its wall consists of large nucleated cells constricted at intervals by strong annular muscles giving a marked ringed appearance externally.

The Malpighian Tubules (Pl. XI, *mt*). Ceratopogonines have departed from the almost universal rule among dipterous larvae in that they possess two or three malpighian tubules instead of four. The Cecidomyids are the only other group of Diptera that show a similar reduction; the Coccids have only two, but these arise as a single tubule which divides at a short distance from its point of origin. The first mention of this condition in Cecidomyids was made in a note by Giard (1893) but he misinterpreted what he found, describing the two malpighian tubules as joined in a loop, and the proctodaeum as exceedingly short. He figured *Diplosis* but says that the same condition exists in all the Cecidomyids he examined, whereas I find in all the species I can procure (not *Diplosis*) that there is a well-developed hind-gut with the three divisions, ileum, colon, and rectum, distinct, and that the two malpighian tubules arise laterally from the most anterior portion of the ileum with their free ends attached to the extremity of the hind-gut as is usual in dipterous larvae. These attached ends Giard took for their origin, hence the supposed shortness of the proctodaeum. Williams (1910), in his paper on the anatomy of *Cecidomyia resinicoloides*, opposed Giard's view, figuring an arrangement of malpighian tubules and hind-gut very similar to that of the forms I have examined. *Miastor* is an exception in this family, having the normal four tubules (Kahle, 1908).

From the examination of all available material it appears that Ceratopogonines are divided fairly evenly in possessing two or three malpighian tubules, but *Forcipomyia* is the only genus in which I have found both conditions occurring. The possession of three is unique among insects; Berlese (1909) quotes *Culex* and *Psychoda* with five as the only known examples of "oligonephrous" insects with an unequal number of malpighian tubules, to which may be added *Anopheles*, *Ptychoptera*, and the Blepharoceridae, all with the same number. In these the odd one is dorsal, but in Ceratopogonines it is ventral.

In *Forcipomyia bipunctata* there are only two. They arise dorso-laterally at the junction of the mid-gut and the hind-gut and, curving outwards and downwards, pass forward along the mid-gut to the mesothoracic segment, where they bend sharply back and return parallel with and above the forward running portion. They pass into the posterior extremity of the body and terminate in the last abdominal segment on either side of the rectum, to which they are attached by strands of connective tissue. They are of no distinctive colouring, and are smooth and straight.

The Salivary Glands (Pl. XI, figs. 8, 9, 12; Pl. XII, *sg*) are two flattened, S-shaped bodies closely adhering to the walls of the mid-gut at its anterior extremity. The salivary duct (*sd*), thin-walled and ringed like a trachea, extends from the front of the hypopharynx to a point in front of the first thoracic ganglion, where it forks, the branches passing on either side of the nerve connectives to the glands. The anterior portion of the gland consists of a mass of uninuclear cells, which pass posteriorly into a flattened condition in which a row of very large binucleate cells occurs on either side of a clear central channel (Pl. XI, fig. 8); each cell is also separated by a smaller clear area. This arrangement of cells exists to the sharp tip of the long upper arm of the S, which lies along the dorso-lateral surface of the mid-gut. The nuclei are large, and the chromatin occurs in conspicuous granules, not in a ribbon as in *Chironomus*.

Nervous System.

The Central Nervous System (Pls. XI, XII) consists of a brain (*br*), a sub-oesophageal ganglion (*sog*), and a ventral chain of ten ganglia, three thoracic and seven abdominal.

The Brain is of the normal bilobed form found among dipterous larvae, but it is situated in the prothorax, there being no room for it in the head on account of the space taken up by the hypopharynx and its tremendous muscles; indeed this condition seems to be the rule among Chironomid larvae even when the hypopharynx is absent. The lobes of the brain are joined together broadly in front, and the *crura cerebri* connecting with the sub-oesophageal ganglion are very large and thick. The antennary nerves (*ann*) pass through the pedunculate cephalic imaginal discs, which are elongated so as to invest the nerves almost up to the antennae; the size of the antennary nerve indicates an important function of that organ. The optic nerve, on the other hand, is so small that it could not be traced more than a short distance from the eye.

The Suboesophageal Ganglion lies beneath and partially in front of the lobes of the brain; from its anterior margin two large nerves pass into the head and branch several times to supply the hypopharynx and mouth-parts. The nerves to the latter form small ganglia before proceeding to the sensory organs.

The Ventral Chain. A very short pair of connectives lead from the sub-oesophageal ganglion to the first thoracic ganglion, in the prothorax, directly above the pseudopod. The second thoracic ganglion lies in the posterior part of the floor of the mesothorax, joined to the first by a pair of widely separated connectives which give passage to two pairs of muscles. The third thoracic ganglion occupies a position in the front of the metathorax, and the abdominal ganglia occur in a corresponding position in each segment back to the fifth. This segment contains the fifth abdominal ganglion in its anterior portion and the sixth at its posterior margin, while just across the dividing line in the sixth segment the seventh ganglion is found. This last is larger and longer

than the preceding ones and represents a fusion of the seventh and eighth ganglia, innervating the last two abdominal segments.

The Sympathetic System (Pl. XII). The arched nerves (*arn*) of the Stomatogastric System may be traced up through the sides of the head, passing inwards over a small muscle arising on the roof of the head and attached to the tip of the lateral wings of the hypopharynx, and meeting to form the Frontal Ganglion (*fg*); this is a small triangular mass of ganglion cells situated in the middle of the upper caudal surface of the strong transverse muscle connecting the two lateral wings (*trm*). The origin of the arched nerves on the lobes of the brain has not been satisfactorily established; they should be given off from the top of the *crura cerebri*, but actually they seem to be branches of the large nerves of the suboesophageal ganglion. The recurrent nerve (*rn*) has been traced back from the frontal ganglion along the dorsal surface of the oesophagus to a very small ganglion on the anterior extremity of the cardia, whence nerves proceed along each side of the mid-gut. Beneath the brain the recurrent nerve sends branches laterally to a pair of ganglia lying close to the sides of the mid-gut at its anterior end; these are thin, flat plexuses, not well defined, and the nerves given off from them have not been traced.

Transverse Nerves (Pl. XI, fig. 8, *tn*). From each ganglion of the ventral chain, except the first and ninth, a fine median nerve proceeds backwards between the connectives and forks to join the stouter transverse nerve. These always occur at the junction of the segments, but cannot be demonstrated between the prothorax and mesothorax, seventh and eighth abdominal, or two halves of the eighth abdominal segment. If such exist, as in some Chironomids (Miall and Hammond, 1900), they are too delicate to discern without recourse to special nerve stains.

Circulatory System and Nephrocytes (Pls. XI, XII).

The circulatory system consists of a simple tube, the dorsal vessel (*dv*), running through the entire length of the larva; the anterior extremity is open while the posterior end enlarges to form the so-called heart (*ht*) with valves for the entrance of the blood.

The Heart is a very simple and primitive organ, being nothing more than a slight enlargement of the dorsal vessel, with thin membranous walls; the muscle fibres which must be present in the wall of the heart and dorsal vessel are too delicate to be demonstrated. There are only two valves, situated on either side of the truncated extremity, in the first portion of the eighth abdominal segment. Fortunately the peripheral fat-body is absent in the dorsum of this region, leaving a window through which the action of the heart may be observed in a living larva; were it not for this the number of valves would remain unknown, for they were never seen even in the most careful dissection.

The Dorsal Vessel passes forward above the digestive tract just below the dorsal body-wall as far as the prothorax, where it descends and continues in

contact with the oesophagus into the head. As seen in Pl. XII there is a dorso-ventral enlargement at the point of union with the oesophagus. The portion of the vessel anterior to this point is usually termed the aorta (*aor*); it becomes smaller and passes along on top of the oesophagus between and beneath the lobes of the brain. Within the head it enlarges again dorso-ventrally and separates from the oseophagus; if there is any suspending filament at its termination it is too fine to be detected.

The Alary Muscles (Pl. XI, figs. 8, 10, *am*) which keep the dorsal vessel in place are very delicate fan-shaped muscles occurring segmentally in the abdomen but not in the thorax. They arise at the junction of the segments in every case and pass backward and forward into their respective segments.

The Nephrocytes (Pl. XI, *ne*). The term "nephrocytes" was given to the pericardial cells and others of similar function by Bruntz (1903) after their physiology had been worked out by Kowalevsky, Metalnikoff, Cuénot and others. Keilin (1917) first introduced the term in this country, and gave a full account of the discovery of the function of these interesting cells. Kowalevsky found that when certain coloured fluids were introduced into dipterous larvae, either in the food or by direct injection into the body-cavity, the pericardial cells and others in the thorax and scattered throughout the body took them up, and not having any efferent ducts they retained the foreign matter and remained coloured all their life, even into the adult stage. Ammonia-carmine proved best for this purpose as the carmine precipitates in highly visible granules in the protoplasm of the cells.

In spite of the small size of *Forcipomyia* larvae a few successful injections were performed, in which the larvae remained alive long enough for the ammonia-carmine to be taken up by the nephrocytes, making it possible to study the anterior as well as the pericardial cells.

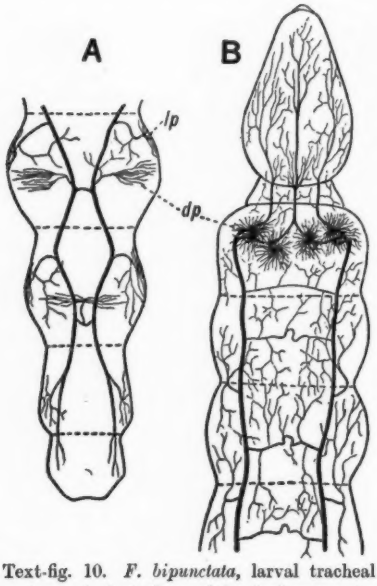
The nephrocytes occur in typical Chironomid arrangement as large, binucleate, or occasionally tri- or polynucleate, cells situated in pairs segmentally on the sides of the dorsal vessel at the point of attachment of the alary muscles, the fibres of which pass above and below them. There are thus four in each abdominal segment but the last. In the thorax there is a double group of cells situated on top of the dorsal vessel just before it joins the oesophagus. Only the posterior half of this mass eliminates ammonia-carmine and is therefore nephrocytic, probably corresponding to the anterior nephrocytes demonstrated by Metalnikoff (1902) in Culicine larvae. The anterior, non-nephrocytic portion may be the fused ganglia of the sympathetic system described by Miall and Shelford (1897) for *Phalacrocera*, or it may be a small imaginal disc, since in very far-advanced larvae there seems to be a long, narrow strip of developing tissue extending back along the dorsal vessel.

Tracheal System (Text-fig. 10).

All the members of the Ceratopogoninae have a closed tracheal system, and it is remarkable that some have adapted themselves to a terrestrial life

without any alteration in this condition. Among Diptera a genus of Mycetophylids, *Ceroplatus* (Keilin, unpublished), and the terrestrial Chironomid, *Camptocladius*, are the only ones to share this phenomenon.

There is a well-developed tracheal system in the form of two main trunks in the dorsum, one on each side of the dorsal vessel, extending throughout the full length of the body (Pl. XI, fig. 8). Near the front of each segment a lateral branch passes down to supply the ventral part of the body, and slightly further back a transverse branch connects the two trunks above the dorsal vessel. In the prothorax the lateral trunks send branches inwards which unite just behind the brain, and the common trachea passes between the lobes into the head; it runs up over the hypopharynx and down into the front region of the head, giving off branches all the way. The lateral trunks in the prothorax converge slightly and drop down, passing into the head at a lower level than the median trachea. Four radiating plexuses occur in the prothorax just below the dorsal cuticle (*dp*), while in the abdomen, beginning with the second segment, there is a small dorsal plexus arising from the transverse connecting tracheae of each segment, and also a small lateral one (*lp*). In the last segment the main trunks taper off and terminate in fine tracheae.



Text-fig. 10. *F. bipunctata*, larval tracheal system. A, last three abdominal segments; B, head and thorax. *dp*, dorsal plexus; *lp*, lateral plexus.

Muscular System.

Throughout the abdomen there is a longitudinal band of muscles in the dorsum on either side of the dorsal vessel, extending part-way down the sides, and a latero-ventral band on either side of the ventral nerve chain. No transverse or dorso-ventral muscles occur in the abdomen, for the larva is of sluggish habits and does not need a complex muscular system in the abdomen. A single diagonal muscle crosses the latero-ventral bands of each segment from the dorsal side behind to the ventral side in front, and another pair terminates in the middle of the segment beneath the nerve connectives. There is a median muscle attached to the dorsum of the ultimate segment, passing down to the anus to retract the anal blood gills.

In the thorax the musculature becomes more complex owing to the presence of the pseudopod. There is no change in the metathorax except that the diagonal muscles extend into the mesothorax and converge to pass between

the widely separated connectives of the pro-mesothoracic ganglia, terminating at the posterior edge of the orifice of the pseudopod. Two diagonal muscles arise from each side of the mesothorax at its posterior margin and are attached in the pseudopod at its point of bifurcation; one pair of these passes between the connectives of the ventral chain with the pair previously described. There is no band of latero-ventral muscles in the pro- or mesothorax, but the dorsal bands continue throughout. The other retractor muscles of the pseudopod consist of a short pair arising at the point of bifurcation and passing back to the posterior margin of the prothorax, and three long ones on either side of the body passing from the extremity of the forks of the pseudopod up to the dorsum. The pseudopod is apparently protruded by pressure of the blood brought about by contraction of the body muscles. Other muscles in the prothorax may be seen in Pl. XII.

In the head the musculature is exceedingly complicated; Pl. XII shows all the principal muscles of one-half of the head, but there are other small ones whose exact nature and function it has been impossible to determine. Most noticeable is the large fan-shaped muscle (*pm*) composed of five lamellae in the posterior part of the roof of the head which attaches to the base of each wing of the hypopharynx and draws back the whole dorsal portion in the process of mastication. This muscle is opposed by a lesser anterior one (*adm*) which serves to bring the grinding portion of the hypopharynx forward again. The third important muscle of the hypopharynx is that which joins the two lateral wings, shown in transverse section in Pl. XII (*trm*); contraction of this muscle, drawing the wings together, would elevate their tips slightly but with great leverage; this elevation would be transmitted by the chitinous suspension rods (*sr*, Pl. X, figs. 2, 3) to the ventral portion of the hypopharynx, thus decreasing the interval between the grinding surfaces. A pair of short muscles with wide base on the floor of the head holds the ventral portion in position.

A number of narrow muscles pass from the posterior dorsal margin of the head to the oesophagus, and others from the roof of the head to the dorsal wall of the mouth cavity, for the purpose of distending the oesophagus and increasing the capacity of the mouth. For the operation of the mouth-parts there are a number of muscles in the sides and top of the head. The premandibles are worked by a pair of longitudinal muscles (*pmm*) in the roof of the head which are not like other muscles but seem to be enclosed in a thick sheath; they connect with the upper extremity of the premandibles by a long tendon. The mandibles are operated by two sets consisting of three and four muscles respectively, attached along the sides of the head and converging until they unite in tendons, by which they are attached to the proximal end and the middle of the mandible. There is in addition one pair of muscles passing from the sides of the head down to the papillate area of the labrum to give mobility and control to that organ.

Oenocytes.

In Dipterous larvae there are commonly found two kinds of oenocytes, a large, arranged segmentally in groups, and a small, with more or less scattered disposition. They are cells in close connection with the hypodermis, of homogeneous cytoplasm, sometimes slightly vacuolated, with a distinct small or very large nucleus, and they are always attached to tracheae or invested by tracheoles. Their affinity for stains and the absence of oil droplets makes them readily distinguishable from the surrounding fat-body.

In *Forcipomyia* the large oenocytes occur as a paired, sub-spherical group of four cells in the middle of each of the first seven abdominal segments, directly laterad of the upper margin of the latero-ventral muscle bands. No fifth, separate, binucleate cell occurs in front of the group as in *Chironomus* (Miall and Hammond, 1900), and I have been unable to distinguish the small variety of oenocytes at all.

Fat-body.

Adipose tissue fills the space between the body wall and the longitudinal muscles in each segment, and surrounds the ventral nerve chain. The perivisceral fat-body is in the form of a long, thick, irregular ribbon lying along each side of the intestine. There is no difference in the histological structure of the peripheral and perivisceral fat-bodies; both consist of large thin-walled cells containing a small nucleus, granules of protein, and droplets of oil.

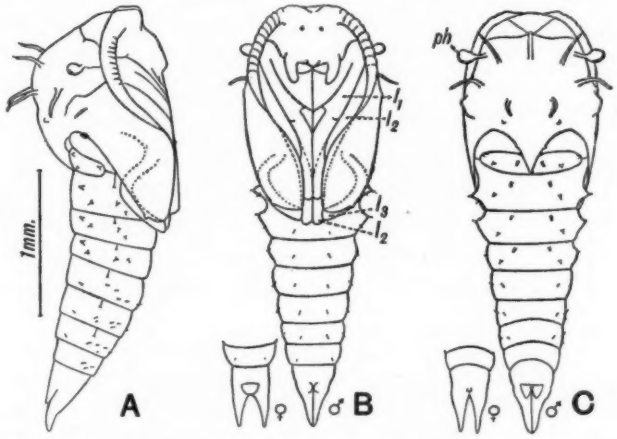
Gonads.

The rudimentary sexual organs are a pair of pyriform bodies attached by strands of connective tissue to the sides of the hind-gut in the seventh abdominal segment (Pl. XI, figs. 8, 11, 12, *gn*). From the anterior pointed end a long filament passes forward to the junction of the fourth and fifth segments in the dorsum. Behind, a short filament leads to a second pair of bodies (*fb*) rather shorter and rounder, which appear to be composed of adipose tissue cells; these probably play an important part in the development of the imaginal structures, but their function has not been determined.

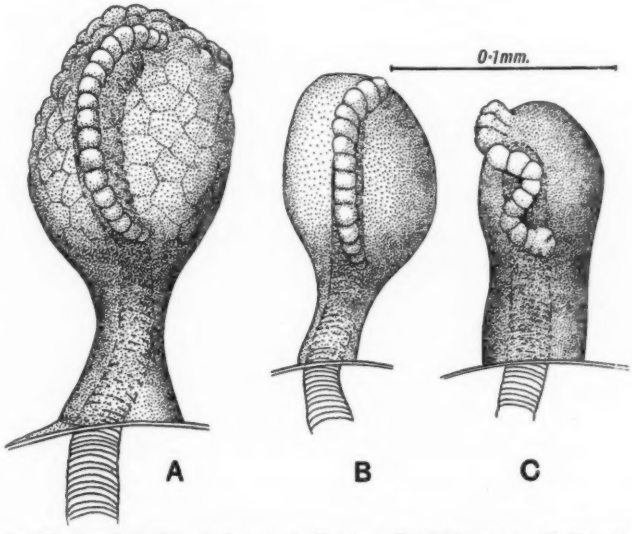
(B) PUPA.

The pupa when removed from its larval skin measures 2·8 mm. to 3·0 mm. in length and 1·0 mm. in width at the thorax. The cuticular spines and the prothoracic horns constitute the principal taxonomic characters (Text-fig. 11). On the dorsum of the thorax there are three pairs of long, slender, tapering spines, the anterior pair bearing at the tip a short sensory hair. In some species a fourth posterior pair is present, but in *bipunctata* these are represented by small tubercles. A fifth still smaller pair of tubercles occurs on the sides of the median posterior prolongation of the thorax in all *Forcipomyia* pupae, and it is noteworthy that spines replace these papillae in many species of *Atrichopogon* (*rostratus* and exotic species not yet named). The first four

segments of the abdomen carry each a pair of very short spines on the dorsum, and further apart a pair of short sensory setae set on papillae; similar papillate setae occur on the sides. Behind the fourth abdominal segment, *i.e.* the portion



Text-fig. 11. *F. bipunctata* pupa. A, lateral. B, ventral. C, dorsal view. $l_1, _2, _3$, first, second and third pairs of legs; *ph*, prothoracic horn.



Text-fig. 12. Pupal prothoracic horns. A, *F. picea*. B, *F. bipunctata*. C, *F. radicicola*.

covered by the larval skin, only simple microchaetae occur. Though the pupa is propneustic traces of the rudimentary closed spiracles can be discerned on the pleurae of the abdomen as also may be seen in other Chironomids (Potthast,

1915, *Orthocladius*; Thienemann and Zavrel, 1916, *Tanypinae*). The last abdominal segment is medially divided in its distal half into two tapering processes, closely approximated in the male and widely separated in the female.

The Prothoracic Horns (Text-fig. 11, *ph* and Text-fig. 12, B) are knob-shaped, on a short stem; a curving row of about fourteen spiracular papillae (de Meijere, 1902) occurs on the posterior side. The remainder of the knob is composed of smooth chitin, in marked contrast to the papillate, reticulate condition found in some other species (*picea, pulchrithorax*).

II. *Forcipomyia picea* (Winnertz) 1852.

F. latipalpis (Kieffer) 1901.

F. corticicola (Kieffer) 1919.

I have reared this species repeatedly from many localities around Cambridge, and other places as listed below.

From Kieffer's own figures and description of the larvae and pupae of *latipalpis* it is quite plain that he was dealing with *picea*. With regard to *corticicola*, Rieth's (1915) figures are suggestive but do not furnish positive proof; however I have examined all the stages from material labelled *corticicola* in the Thienemann collection in the British Museum and find them identical with *picea* in every respect.

Perris' *laboulbeni* (1870) was in all probability *picea*, but no material now exists, and the descriptions are insufficient proof.

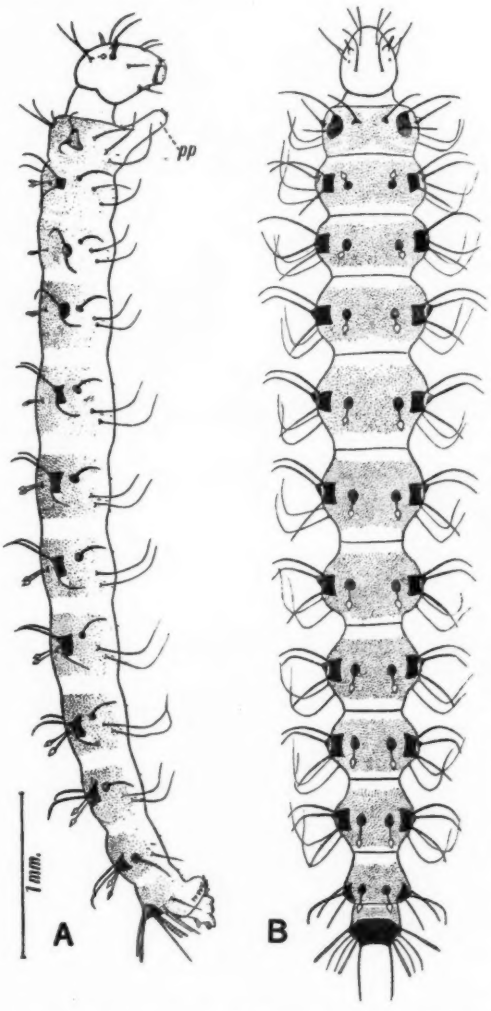
This species is strictly bark-inhabiting; I find it quite commonly under the loose bark of almost any tree, coniferous or deciduous, if it has been felled long enough and the conditions are suitable for the development of the moulds and fungi which serve as food. Larvae and pupae were taken at Cambridge, near Bishop's Waltham, Hants., near Painswick, Gloucs., and at Hampstead, London.

(A) LARVA. (Full-grown.)

The larvae (Text-fig. 13) are somewhat larger than those of *Forcipomyia bipunctata*, measuring 5 mm. to 6 mm. when fully grown. After a little practice they may be separated from that species with the naked eye by their more translucent, less chalky colouring. There is a definite colour pattern in brownish grey on the vertex of the head (Text-fig. 14, C) disposed according to the origin inside the head of the lamellae of the large posterior muscles of the hypopharynx. A slight difference occurs in the antennae (Text-fig. 14, A), the elliptical opening being shorter and the apical projection much smaller. There is a distinct frontal suture on either side of the head running back from the antennae (Text-fig. 14, C, *fs*) along which the head splits at pupation.

The Mouth Parts are identical in the two species except that the dorsal grinding surface of the hypopharynx of *picea* is studded with rows of minute, rounded, tooth-like projections (Pl. X, fig. 7) instead of the three transverse ridges of *bipunctata*.

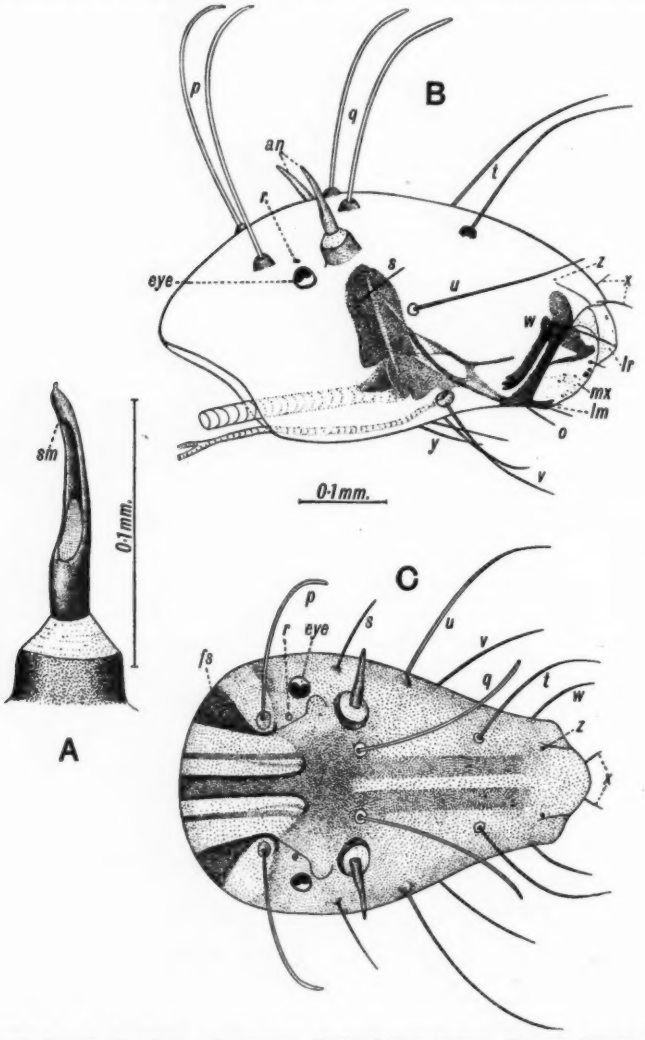
The Prothoracic Pseudopod (Text-fig. 15) offers a specific character in that the two branches do not separate widely, and are broad at the extremity; the crown of hooks is situated on the inner side.



Text-fig. 13. *F. picea* larva. A, lateral. B, dorsal view. *pp*, prothoracic pseudopod.

The Chaetotaxy (Text-figs. 14, 16) presents the simplest, surest, and most obvious means of identifying the species. On the head the disposition of the hairs and pits is normal, but the hairs *p* and *q* are long, curving, and simple

instead of the enlarged lanceolate form found in *bipunctata*. The same substitution occurs on the prothorax. Throughout the body there is the same number of hairs to a segment as in *bipunctata* but with the important difference



Text-fig. 14. *F. picea* larva. A, antenna. B, head, lateral view. C, head, dorsal view. (For lettering see Text-fig. 4.)

that two of the lateral hairs arise from a common base; from their position it seems probable that the hairs *b* and *d* are the two involved. In the ultimate segment the lanceolate hairs are again replaced by stout, simple hairs, and the

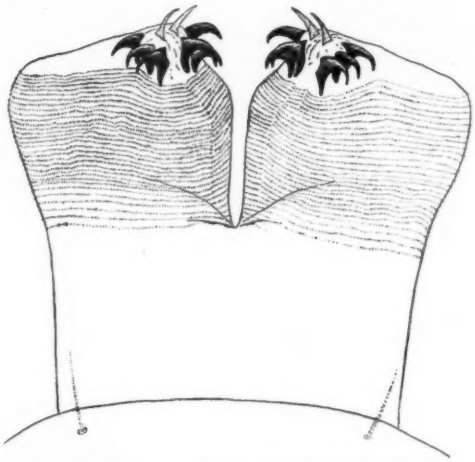
whole dorsum of the last half of the segment is covered with a cap of dark chitin, from which three pairs of hairs arise (Text-fig. 16, A). Some time previous to pupation the *a* hairs of each segment become connected by a transverse bar or thickening of the integument, as in *bipunctata*; these are only distinct from the second abdominal segment backward.

Anal Blood-gills bilobed.

Number of *Malpighian Tubules* three (Pl. XI, fig. 11).

(B) EARLY LARVAL STAGES.

By good fortune, after much fruitless searching, larvae of the first summer generation were found under bark (Cambridge, 15. v. 23) in their first stage, so it has been possible to study the morphological changes in all the larval stages and to record the time occupied by each. In spite of careful search



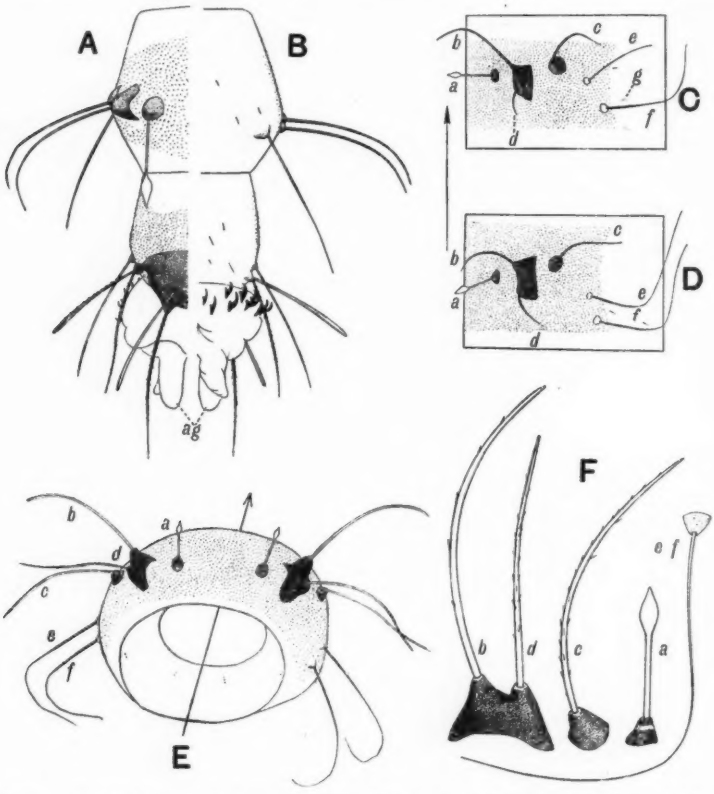
Text-fig. 15. *F. picea* larva. Prothoracic pseudopod.

eggs or empty egg-shells could not be found; they are probably laid in crevices in the bark, and the larvae on hatching proceed to their normal habitat between the wood and the bark.

The *First Stage Larvae* (Text-fig. 17, B) are minute, colourless, and refractive, measuring about 1 mm. long when ready to moult. They show many interesting variations in chaetotaxy from the full-grown larvae.

The Head (Text-fig. 17, C, D) is normal in shape and has all the usual hairs with the exception of *q*; *p* is present, rather long with a more swollen tip than in later stages, but there is no *q* between or just in front of the antennae. The only other pair on the front is stout and black, with very fine lateral setae; they are much more likely to represent the *t* hairs moved up than the *q* hairs moved down, for all the *a* hairs of the body and the *p* hairs of the head are distinctly lanceolate, even though simple in later stages.

The Antennae are comparatively long, situated upon very slightly raised bases. In the middle of the vertex there is a diamond-shaped raised area culminating in a sharp chitinous tooth, the *Egg-burster* (Text-fig. 17, C, D, *eb*). Similar structures exist in most eucephalous dipterous larvae, notably in

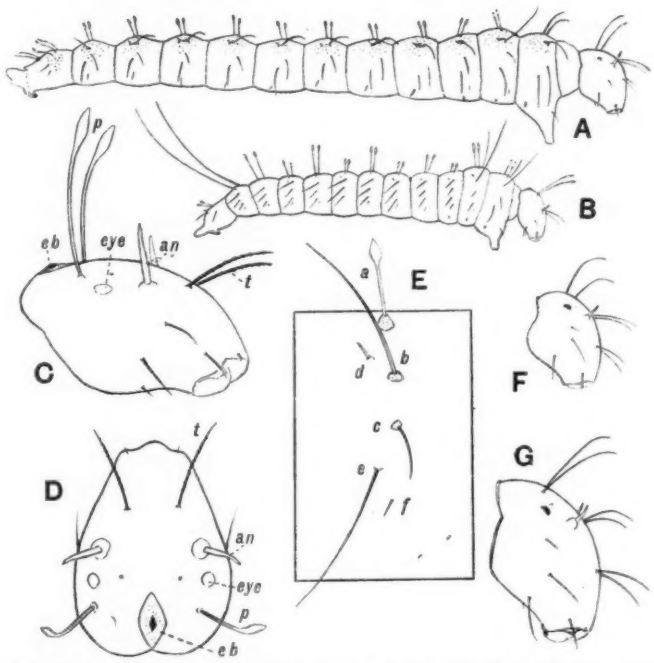


Text-fig. 16. *F. picea* larva. A, dorsal, B, ventral view of eighth abdominal segment. C, setal plan of mesothorax. D, setal plan of second abdominal segment. E, perspective drawing of single abdominal segment. F, macrochaetae of a segment, highly magnified. (For lettering see Text-fig. 7.)

Culicidae, Mycetophylidae, Simuliidae, and some Chironomidae (Edwards, 1919).

On the *body* the chaetotaxy differs from that of the fourth stage larva in the following points: the *a* hairs of the prothorax are lanceolate, not simple; those of the remaining segments are of different lengths, but the variation is constant. On the first half of the eighth segment the *a* hairs are represented by a pair of very long, slender, simple, curving hairs (Text-fig. 17, B), similar to those found in *Phlebotomus* larvae, though in that genus the two of the

first stage become four in the last (Newstead, 1911). In some exotic forms of *Forcipomyia* to be described in a subsequent paper similar hairs are retained until pupation. The *b* and *d* hairs are not united basally; *d* is absent on the prothorax, and present on the other segments only as a minute straight spine (Text-fig. 17, E). On the pro- and mesothorax the *b* hairs are very slender and elongated. The presence in young larvae of longer hairs than in later stages is of quite frequent occurrence among Nematocera, *e.g. Bibio* (Morris, 1921), and



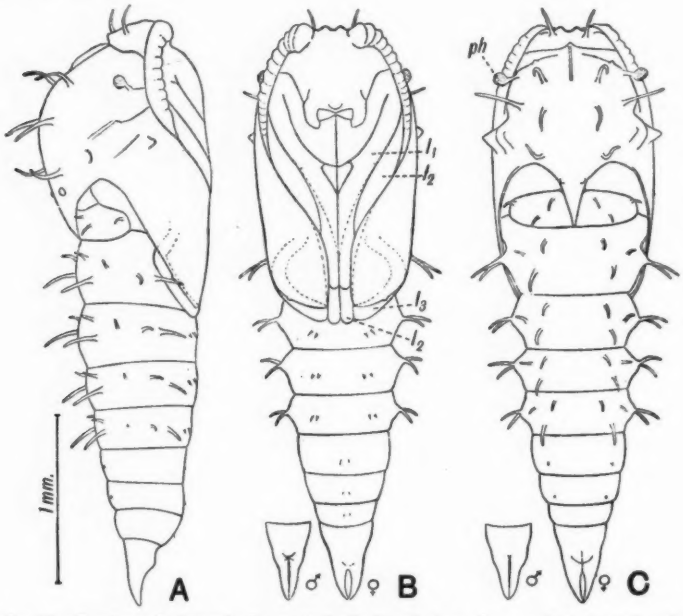
Text-fig. 17. *F. picea*, early larval stages. A, second stage larva. B, first stage larva. C, head of first stage larva, lateral. D, dorsal view. E, setal plan of second abdominal segment of first stage larva. F, head of third stage larva. G, head of fourth stage larva. (A, B, F and G all drawn to same magnification); *eb*, egg-burster.

Cyclorrhapha Aschiza (Keilin, 1911, 1915, *Phoridae*, *Syrphidae*). The *f* hairs are present as very small spines, almost microchaetae. The lateral thoracic groups of sensory hairs, rudimentary sense organs of the absent legs, are present as in older larvae. Cuticular armature is absent in the first stage.

Miall and Hammond (1900) state that in *Chironomus* the brain is contained in the head in the first stage, and moves back into the thorax after the first moult. This is certainly not the case in *Forcipomyia*, the brain occurring in the prothorax and mesothorax from the very first, proportionately much larger in the first than in later stages.

In the *Second Stage* (Text-fig. 17, A) the *q* hairs of the head appear; both *p* and *q* have swollen tips. The vertex loses all signs of the egg-burster. The *a* hairs of the body all become equal in length, the prothoracic pair losing the swollen tips and becoming simple hairs. The hairs *b* and *d* join up basally on all segments except the prothoracic where *d* is still lacking. The *f* hairs remain as microchaetae. Dorsal cuticular armature appears.

In the *Third Stage* the *d* hairs of the prothorax appear, the *f* hairs assume the same length as *e*, and in fact the entire chaetotaxy resembles that of the full-grown larva.



Text-fig. 18. *F. picea.* A, lateral. B, ventral. C, dorsal view. $l_{1, 2, 3}$, first, second and third pairs of legs; *ph*, prothoracic horn.

(C) PUPA.

The pupa also is larger than that of *bipunctata*, measuring about 3·5 mm. and it is slightly narrower and more slender. The cuticular spines are larger and more numerous (Text-fig. 18). On the head there is a short pair projecting forwards, and on the thorax there are four pairs, the fourth being represented in *bipunctata* by papillae. On each segment of the abdomen but the first and the four last, which are covered by the larval skin, there are two dorsal pairs, one dorso-lateral pair, and two lateral pairs, all elongated and slender; on the venter two pairs of small spines surmounted by short sensory hairs occur. There are no lateral or ventral processes on the first, and no ventral on the second abdominal segments on account of the overlapping wing cases. The

portion within the larval skin bears no dorsal or lateral microchaetae as in *bipunctata*, but a single pair of very short dorsal processes occurs on the sixth and seventh, and the sixth, seventh, and eighth bear a pair of ventral microchaetae. The terminal appendages of the female are contiguous at the tip.

The Prothoracic Horns (Text-fig. 12, A) are remarkable for the reticulation of the chitin forming the knob; there are about 18 spiracular papillae in a normal curve.

III. *Forcipomyia radicicola* Edwards n. sp.

The larva of a *Forcipomyia*, probably this species, was figured and described by DeGeer (1781) in his *Memoires*; the specimens were from the roots of old Umbelliferae and though the chaetotaxy is not accurate the larva is quite recognisable as a *Forcipomyia*. The species has been repeatedly taken in England in the rotting tap-roots of Umbelliferae (*Angelica*, *Pastinaca*) and *Arctium* (Burdock), but it was only recently recognised as a new species.

Presumably the eggs are laid at the surface of the earth around the root of the plant, for the young larvae are found under the decaying cortex not very far down. As decomposition proceeds they take the first opportunity to enter the hollow heart of the root, where they remain throughout the winter.

(A) LARVA.

The larvae are pure creamy white, but clean specimens are rare; there is usually a quantity of yellowish brown matter adhering to the body. The head is slightly yellowish and has no dorsal markings. The larvae are of medium length, 3·2 mm. to 4·0 mm. when fully grown.

The Prothoracic Pseudopod has not been figured as it is almost identical with that of *F. picea* in the position of the crown of hooks and the nature of the two central ones.

The Anal Blood-gills (Text-fig. 19, F, G, *ag*) are single-lobed.

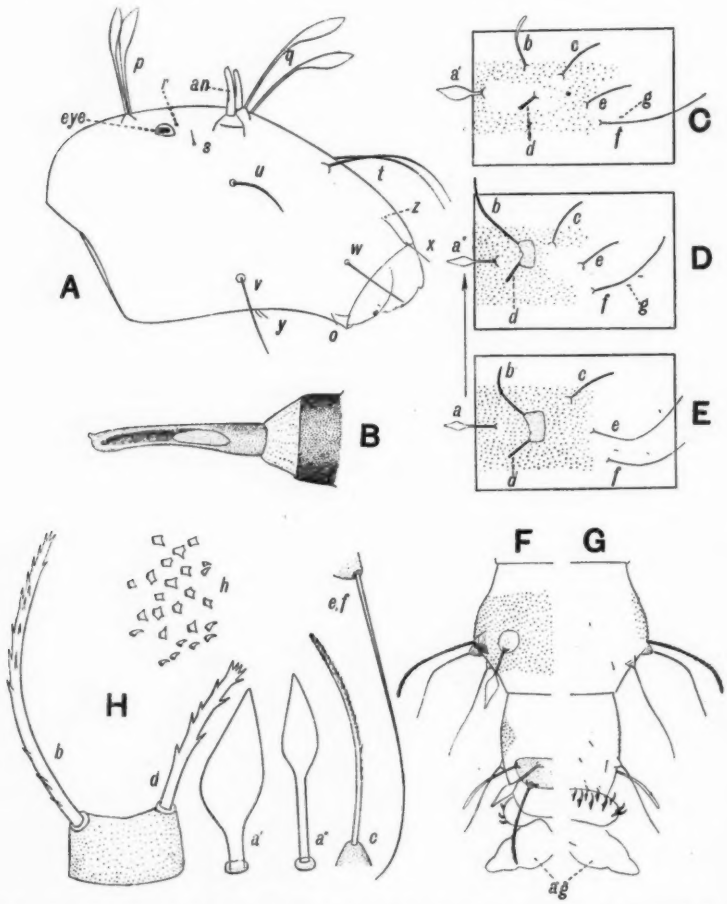
Chaetotaxy. The hairs *p* and *q* of the head are lanceolate. On the body the *a* hairs are also lanceolate, the prothoracic pair very large, with short pedicels (Text-fig. 19, C, H, *a'*); the hairs *b* and *d* arise from a common tubercle on all segments except the prothoracic and eighth abdominal, but the pigmentation is so slight that they are inconspicuous, while the hairs are black. The minute cuticular armature is not simple as in most forms but each projection has two or three points; passing down the pleurae they revert to the common hook form (Text-fig. 19, H, *h*).

Number of *Malpighian Tubules* three.

(B) PUPA.

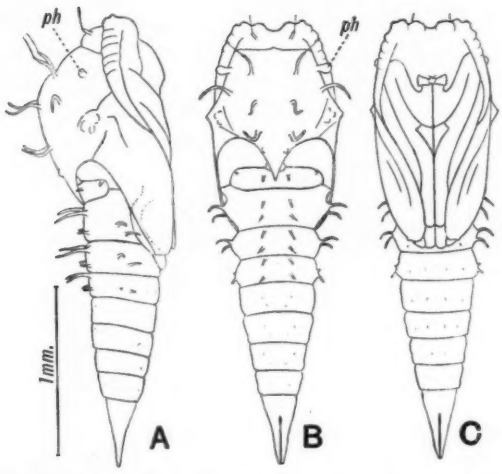
The pupae are found in the same situation as the larvae, often as far up in the crown of the hollow root as they can get. Roots examined in spring frequently disclose adults waiting until decomposition shall furnish them an exit. When removed from their larval skin the pupae measure 2·4–2·7 mm.; they are creamy white at first but soon become grey owing to the black hairs

of the imago developing within. The disposition of cuticular spines is as follows: on the head, one pair with long terminal setae; on the thorax, four pairs, the anterior pair bearing long terminal setae; on the abdomen, segment 1, two small dorsal pairs, segments 2–4, two dorsal and two lateral pairs.



Text-fig. 19. *F. radicicola* larva. A, lateral view of head. B, antenna. C, D, E, setal plans of prothoracic, mesothoracic, and second abdominal segments respectively. F, dorsal, G, ventral view of eighth abdominal segment. H, macrochaetae, highly magnified. *a'*, dorsal lanceolate hair of prothorax; *a''*, corresponding hair of mesothorax. (For other lettering see Text-figs. 4 and 7.)

The Prothoracic Horns (Text-fig. 12, C) are distinctive in the peculiar serpentine twisting of the row of spiracular papillae; the knob is small on a very broad stalk.



Text-fig. 20. *F. radicicola* pupa. A, lateral. B, dorsal. C, ventral view.

IV. *Forcipomyia nigra* (Winnertz) 1852.

This species occurs on the under side of fallen oak and beech branches, on the exposed wet wood, not beneath the bark. So far I have only found isolated specimens hibernating near Cambridge, and am indebted to Mr F. W. Edwards for material collected at Shefford, Beds., and Strelley, Notts., Oct. 1922, and from the collection in the Museum. The immature forms have never been described before.

(A) LARVA.

The living larvae are pale yellowish, somewhat translucent, with conspicuous dark brown basal papillae to the macrochaetae. The head is brown, with a darker V-shaped mark on the vertex and front.

Length of full-grown larva, 3·3–3·7 mm.

The Prothoracic Pseudopod (Text-fig. 21, E) is briefly cleft distally, and the two branches do not separate.

The Anal Blood-gills are single-lobed.

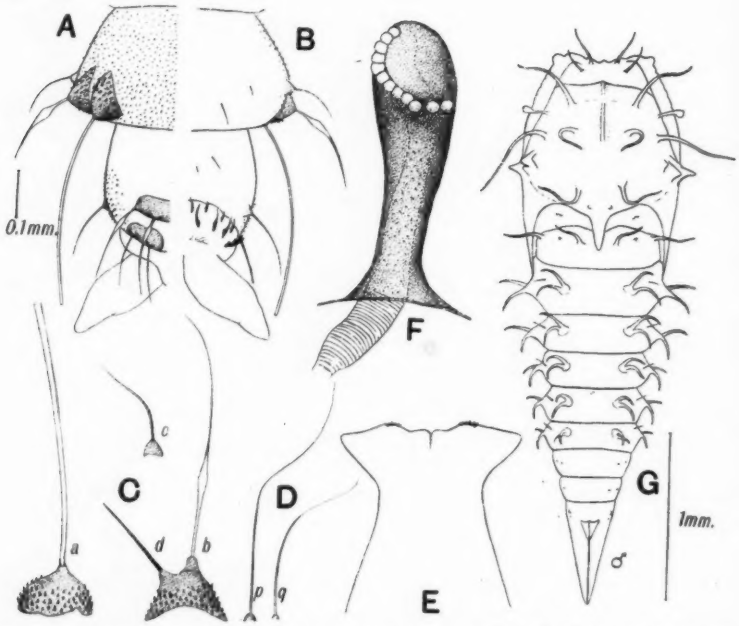
Chaetotaxy. The hairs *p* and *q* of the head are simple, not lanceolate. All the *a* hairs of the body are simple chaetae, not tapering but chisel-shaped at the tip, with a serrate extremity. The hairs *b* and *d* arise from a common basal tubercle as in *picea*, *radicicola*, and others. A strong specific character exists in the presence of cuticular armature part way up on the basal tubercles of the hairs *a* and *bd*. The hair *b* is unusual in being slightly swollen in the middle. The chaetotaxy of the ultimate abdominal segment is of specific importance (Text-fig. 21, A).

Number of *Malpighian Tubules* three.

(B) PUPA.

The pupa (Text-fig. 21, G) is remarkable for the length and profusion of its cuticular spines, which extend to the sixth abdominal segment in two double dorsal rows and one double lateral row. The head bears two pairs, and the thorax four pairs, all long and tapering.

The Prothoracic Horns (Text-fig. 21, F) are much elongated, with a small knob on a long stem; a row of about 12 spiracular papillae curves over the distal end.



Text-fig. 21. *F. nigra.* Larva: A, dorsal, B, ventral view of eighth abdominal segment. C, macrochaetae of the body. D, macrochaetae of the head. E, prothoracic pseudopod. Pupa: F, prothoracic horn. G, pupa, dorsal view.

V. ***Forcipomyia brevipennis*** (Macquart) 1826.

F. lateralis (Bouché) 1834.

F. specularis (Coquillett) 1901.

I have obtained this species many times in the neighbourhood of Cambridge.

For the synonymy of *lateralis* with *brevipennis* I rely on Thienemann's identification of material in the collection named by him in the British Museum. His *lateralis* is undoubtedly *brevipennis*. Bouché's own figures (1834) are of no use as they are incorrect for any possible *Forcipomyia*.

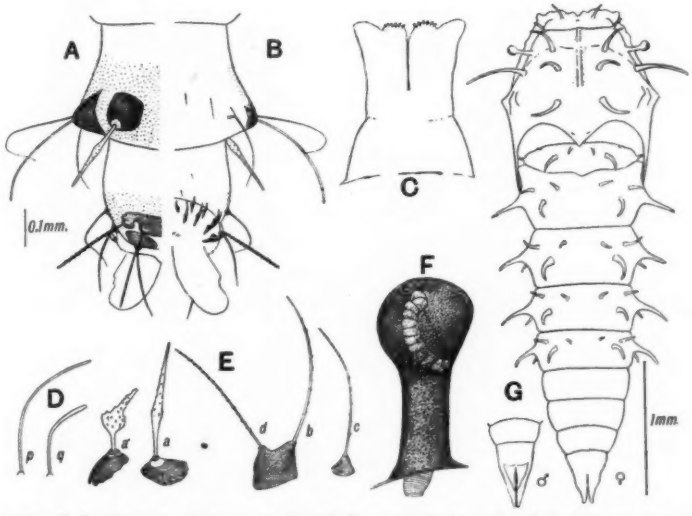
This is one of the commonest species in the genus; it occurs throughout Europe and in North America, but protracted search in its customary habitat

in Brazil during July and August, 1923, failed to reveal the species. It may be found at almost any time during the summer and autumn in drying horse and cow manure, and it hibernates down among the grass roots. I took a single pupa at Hampstead, 14. iv. 23, hibernating inside a potato stem on a rubbish pile, but this seems to be exceptional.

(A) LARVA.

The full-grown larva is large, 5–6 mm. long, dull yellow in colour with the basal papillae of the macrochaetae and the cuticular armature dark brown. The head is brown to black, with a definite colour pattern on the vertex.

The Prothoracic Pseudopod (Text-fig. 22, C) is deeply cleft, but the two branches do not separate; the crown of hooks is placed on the inner angle of each branch.



Text-fig. 22. *F. brevipennis.* Larva: A, dorsal, B, ventral view of eighth abdominal segment. C, prothoracic pseudopod. D, macrochaetae of head. E, macrochaetae of body (*a'*, dorsal hair of prothorax). Pupa: F, prothoracic horn. G, pupa, dorsal view.

The Anal Blood-gills are single-lobed.

Chaetotaxy. The hairs *p* and *q* of the head are simple, though *q* is slightly enlarged distally. On the body the *a* hairs are dull yellowish and quite strongly chitinised, their surface bearing minute hooks or points; they are always flattened, not swollen out as in the majority of *Forcipomyia* larvae. The prothoracic pair (Text-fig. 22, E, *a'*) are short and greatly enlarged in the middle, while those of the remaining segments of the body are longer and less swollen. The hairs *b* and *d* arise from a common basal tubercle. For the chaetotaxy of the last abdominal segment see Text-fig. 22, A.

Number of *Malpighian Tubules* three.

(B) PUPA.

Like the larva the pupa is darker in colour than most species; after the first paleness of pupation it becomes dull yellowish brown, darkening as the adult develops its black hairs within. Cuticular spines are numerous and well developed (Text-fig. 22, G): on the head one pair; on the thorax four large dorsal pairs and a very small pair on the anterior margin; on the abdomen, segment 1, two dorsal and two dorso-lateral pairs; segments 2–5, two dorsal, one dorso-lateral, and two lateral pairs. All the spines are moderate in length, none on the head or thorax bears a terminal seta, and no two of the abdominal ones are joined basally.

The Prothoracic Horns (Text-fig. 22, F) consist each of a spherical, slightly flattened knob on a straight stem, with about 12 spiracular papillae.

VI. *Forcipomyia ciliata* (Winnertz) 1852.

F. boleti (Kieffer) 1901.

F. brunnipes (Perris nec. Meigen) 1847.

F. ciliata occurs rather sparingly in the neighbourhood of Cambridge. The synonymy of *boleti* with this species is evident from Kieffer's description of the larvae and pupae, as also from the description of the adults. The synonymy of the older name *brunnipes* with *brevipennis* is more difficult to establish because the characters were not represented accurately, but the habitat, chaetotaxy, and particularly the bulbous prothoracic horn of the pupa on a very short stem, present sufficient evidence.

This species is usually found upon rotting fungi (Agarics, Polypores, etc.) but during the autumn of 1922 I discovered large colonies of the larvae among rotting waterweed that had been raked from a mill-stream at Great Shelford, Cambs. and thrown over willow logs on the bank. The larvae and pupae were found on the bark of the logs and on pieces of wood in any cavity left beneath the weeds. The following winter hibernating larvae were found inside the rotting stalks of potato plants on a rubbish heap, and beneath the bark of a fallen branch.

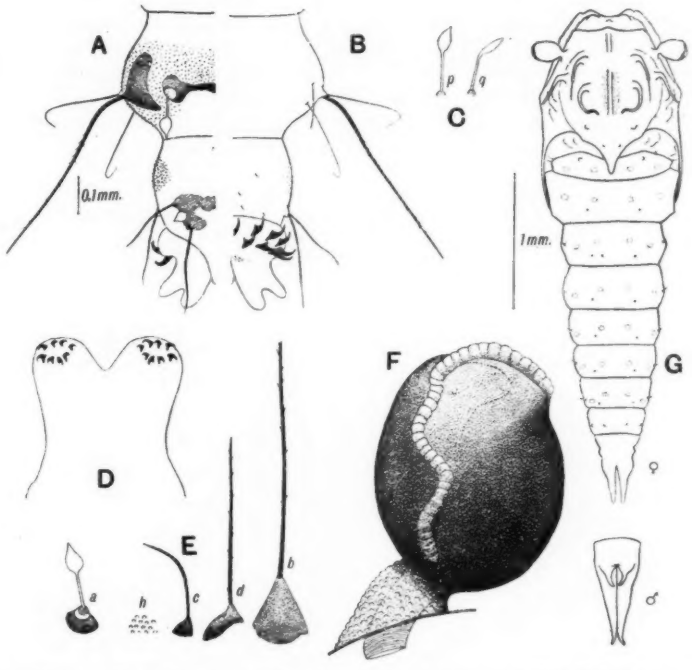
(A) LARVA.

The larvae attain a length of 5 mm., and have a curious habit when disturbed of doubling backwards until the head and tail nearly meet over the back; other species have this habit to a slight extent, but it is most noticeable in *ciliata*. In colour the living larvae are pale creamy white, with the macrochaetae black and their basal papillae brownish grey. The head is pale posteriorly, shading to dark brown around the mouth-parts, with a pronounced frontal V-shaped marking.

The Prothoracic Pseudopod (Text-fig. 23, D) is not deeply cleft, but the two branches separate well, and the crown of hooks surmounts each branch apically.

The Anal Blood-gills are bilobed. The median posterior projection of the dorsum above the blood-gills is unusually large and long. The anterior of the two rows of hooks beneath the anus (posterior pseudopod) only numbers three on each side of the small middle pair, instead of the usual four (Text-fig. 23, B).

Chaetotaxy. The hairs *p* and *q* of the head and the *a* hairs of the body are lanceolate, closely resembling those of *bipunctata*; *b* and *d* are not united basally.



Text-fig. 23. *F. ciliata.* Larva: A, dorsal, B, ventral view of eighth abdominal segment. C, macrochaetae of head. D, prothoracic pseudopod. E, macrochaetae of body. Pupa: F, prothoracic horn. G, pupa, dorsal view.

Cuticular armature two- or three-pointed, star-shaped, not simple hooks (Text-fig. 23, E, *h*).

Number of *Malpighian Tubules* two.

(B) PUPA.

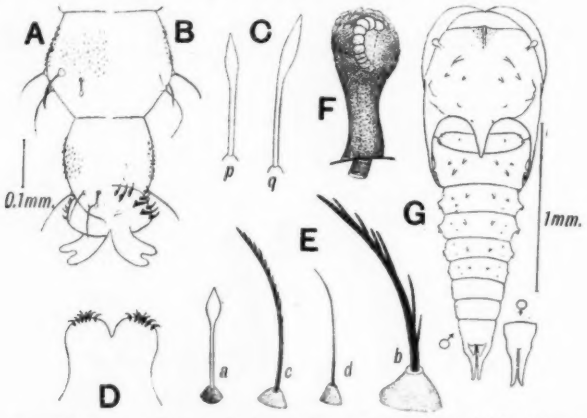
The pupa is yellowish brown in colour. Cuticular spines are strangely lacking (Text-fig. 23, G), there being none on the head, only three pairs on the thorax, and none on the abdomen. The anterior thoracic pair bear long terminal setae; the posterior or fourth thoracic pair is represented only by a pair of low tubercles. On the abdomen a number of regularly placed small ellipsoidal areas may mark the position of suppressed spines, though they

occur also on the segments covered by the larval skin. Microchaetae on the sides are rather more numerous than usual, particularly on the posterior part which retains the larval skin.

The Prothoracic Horns (Text-fig. 23, F) are most distinctive, being in the form of large, slightly flattened, elliptical bulbs on very short bases, with a serpentine row of spiracular papillae roughly 40 in number.

VII. *Forcipomyia pulchrithorax* (Verrall MS.) Edwards n. sp.

This species was first discovered and bred by the late Mr G. H. Verrall in June, 1905, and specimens of the adults were deposited in the British Museum under that name. The species was never described by him so Mr Edwards has kindly supplied a description of the adults to be included here.



Text-fig. 24. *F. pulchrithorax.* Larva: A, dorsal, B, ventral view of eighth abdominal segment. C, macrochaetae of head. D, prothoracic pseudopod. E, macrochaetae of body. Pupa: F, prothoracic horn. G, pupa, dorsal view.

Verrall's records are very brief, and it is difficult to say whether he found the early stages in quite the same habitat as Dr Keilin and I have more recently, namely the granular, solidifying sap in the open wounds of elm, chestnut, and ash trees. The larvae hibernate in this habitat and pass several generations there during the season.

(A) LARVA.

Of all the *Forcipomyia* larvae known in Europe this is by far the smallest species; full-grown larvae only measure 3 mm., and pupae and adults are correspondingly diminutive. They are pale, dull yellow in colour, without dark papillae, so that the stout black macrochaetae *b* stand out conspicuously. The head capsule is almost colourless and the large black hypopharynx shows distinctly in living specimens.

The Prothoracic Pseudopod (Text-fig. 24, D) is of a normal forked nature with the crown of eight hooks surmounting each branch.

The Anal Blood-gills are bilobed.

Chaetotaxy. The hairs *p* and *q* of the head and the *a* hairs of the body are lanceolate. The hairs *b* and *d* are not united basally; *b* is stout and black with spines along one side only. The cuticular armature is comparatively large, the hooks being longer and more slender than usual.

Number of *Malpighian Tubules* two.

(B) PUPA.

Disposition of the cuticular spines as follows (Text-fig. 24, G): on the head, none; on the thorax, three pairs varying greatly in length but never long, the anterior pair terminating in short setae (the fourth may be present or may be represented by a pair of tubercles). On the abdomen the first six segments bear a regular number of processes varying in length from tubercles to short spines.

The Prothoracic Horns (Text-fig. 24, F) are of the normal knobbed type, but they are distinctive in having the distal surface papillate. A row of about ten spiracular papillae occurs on the knob in a simple curve.

VIII. *Forcipomyia braueri* (Wasmann) 1893.

This myrmecophilous form was discovered by Wasmann under stones on nests of *Formica fusca* at an altitude of 5500 feet at Lech in Vorarlburg, August, 1891 (Wasmann, 1893). Through Dr Wasmann's kindness in lending me material I am able to give the specific characters of the larva; no pupae were present in the collection he sent. One record exists of a myrmecophilous form in England other than the more common *F. myrmecophila* (Donisthorpe, 1919). These were pupae taken under a boulder in a *Formica fusca* nest in the Yorkshire moors at Grassington near Keighley by Mr R. Butterfield, 5. v. 19; only one adult was bred out, and this was identified as *braueri* by Mr J. E. Collin, Newmarket. The remaining pupae were saved by Mr Butterfield, Curator of the Corporation Museum at Keighley, and he has kindly given me a specimen to examine. By studying the characters of the attached larval skin I have verified Collin's determination of the species as *braueri*, and I am therefore enabled to include the pupal characters.

(A) LARVA.

Length about 5 mm. Colour pale throughout, including head. Macrochaetae all pale except *c* and *d* which are black; even the basal papillae show scarcely any colour.

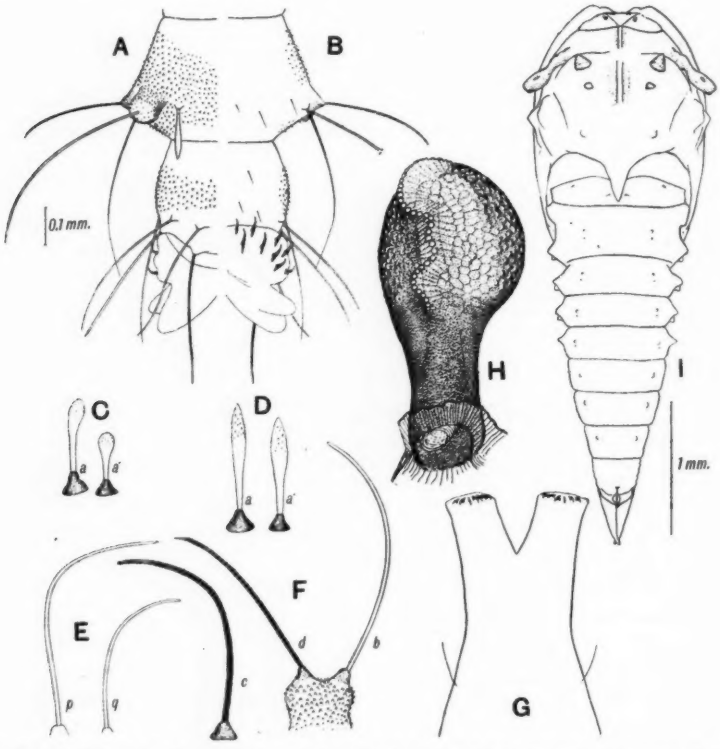
The Prothoracic Pseudopod (Text-fig. 25, G) is uncommonly long, well forked, with the crown of hooks distributed over the entire distal surface.

The Anal Blood-gills are bilobed.

Chaetotaxy. The hairs *p* and *q* of the head are simple, long, and curving. The *a* hairs of the body show two distinct forms which cannot have originated one from the other under any temporary external influence: of the five larvae

from Wasmann three carried bulbous *a* hairs (Text-fig. 25, C) and two had blade-shaped or lanceolate hairs (D); (the English specimen had bulbous hairs). Further breeding and observation is necessary to explain this singular variation. The hairs *b* and *d* arise from a common tubercle situated on a large latero-dorsal evagination; the size and prominence of these tubercles is most striking.

Maceration of the internal organs rendered dissection for the *Malpighian Tubules* impossible.



Text-fig. 25. *F. braueri*. Larva: A, dorsal, B, ventral view of eighth abdominal segment. C, D, the two distinct types of dorsal *a* hairs (*a'*, prothoracic hair). E, macrochaetae of head. F, macrochaetae of body. G, prothoracic pseudopod. Pupa: H, prothoracic horn. I, pupa, dorsal view.

(B) PUPA.

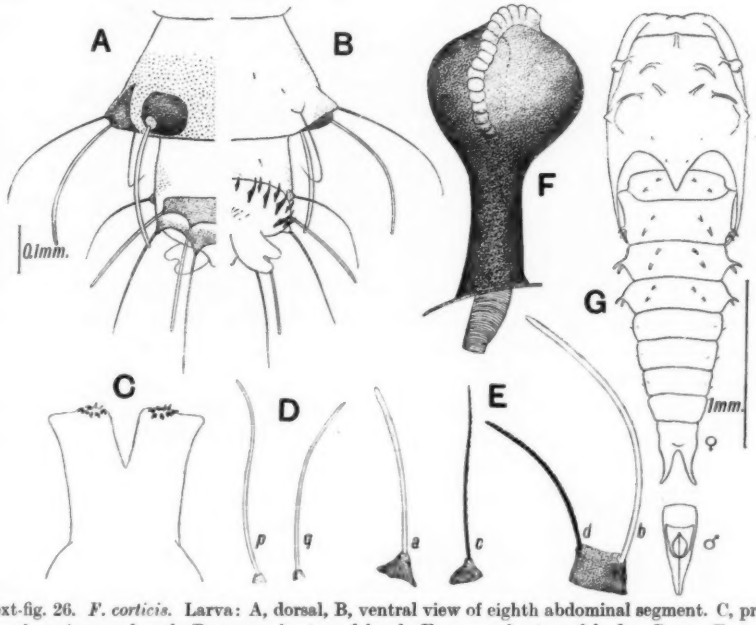
The pupa (Butterfield's specimen) is unusual and most distinctive in form (Text-fig. 15, I); it is large and broad, and is darker in colour than most *Forcipomyia* pupae. There are no cuticular spines, these being replaced by conical tubercles as follows: on the head, two pairs, very small; on the thorax, two pairs, the anterior pair in the form of large cones, the others small (papillae represent the third and fourth pairs of spines); on the abdomen, two pairs of

minute dorsal tubercles and two large conical lateral pairs on segments 2–5, a single minute dorsal pair on 6–8.

The Prothoracic Horns (Text-fig. 25, H) are flattened backwards on the sides of the thorax; the entire surface of the bulbous portion is reticulated and papillated. About 35 spiracular papillae form a serpentine row up the side and over the end.

IX. *Forcipomyia corticis* (Kieffer) 1911.

For the opportunity to examine specimens of this species I am indebted to Mr Edwards who has sent me material from the Thienemann collection in the British Museum. It has not been recorded in England.



Text-fig. 26. *F. corticis.* Larva: A, dorsal, B, ventral view of eighth abdominal segment. C, prothoracic pseudopod. D, macrochaetae of head. E, macrochaetae of body. Pupa: F, prothoracic horn. G, pupa, dorsal view.

The early stages occur beneath the bark of trees and logs (Rieth, 1915), but no particular kind of tree is mentioned. In the same tube with the *corticis* specimens were one larva of *F. nigra* and one pupa of *F. picea*, both of which species live under bark.

(A) LARVA.

Fixed and preserved larvae measure 4–4·3 mm. In colour they are dull yellowish with the papillae of the macrochaetae brown; of the macrochaetae themselves only *c* and *d* are black, the others being golden brown. The head is brown with a definite colour pattern on the vertex.

The Prothoracic Pseudopod (Text-fig. 25, C) is well branched, the terminal hooks being concentrated on the inner margin of each branch.

The Anal Blood-gills are bilobed.

Chaetotaxy. The hairs *p* and *q* of the head are simple, long and slender, but not swollen. The *a* hairs of the body are simple, short and broad but nowhere swollen. The hairs *b* and *d* arise from a common tubercle.

Number of *Malpighian Tubules* three.

(B) PUPA.

The pupa is of the normal yellowish brown colour. The head is devoid of cuticular spines (Text-fig. 26, G). The thorax bears three pairs, the anterior pair with very short apical setae, and a pair of tubercles in place of the fourth pair. On the abdomen there are two dorsal pairs of spines on the first four segments, and two pairs of lateral ones on segments 2–4.

The Prothoracic Horns (Text-fig. 26, F) are of the common knobbed form on a slender stem, with a curved row of nearly 20 spiracular papillae.

SUMMARY.

(1) *Forcipomyia* is one of the few genera of the Ceratopogoninae (Chironomidae) whose larvae are not aquatic. They retain, however, the apneustic condition typical of the entire family, and are therefore compelled to live in moist places such as beneath the rotting bark of fallen trees, in the hollow tap roots of dead plants, in wounds and rot holes in trees, in drying horse and cow manure, in decaying fungi, and in the nests of ants. The immature forms are strongly gregarious.

(2) The larvae pass through four stages, each lasting about a week; the successive changes in chaetotaxy at each moult is recorded in the discussion of *F. picea*. All known European species of this genus hibernate as third or fourth stage larvae. The duration of the pupal stage is about one week; the length of life of the adult has not been determined. There are usually three generations per annum. The adults are known to suck the blood of other insects.

(3) The larvae are eucephalous, more or less cylindrical, 3–6 mm. long, with eleven clearly defined segments (three thoracic and eight abdominal, the eighth divided into two apparent segments). Progression is achieved by means of a retractable, biramous, *prothoracic pseudopod*, and a ventral hook-studded ridge on the ultimate abdominal segment, with the occasional aid of the mandibles.

(4) The head and body bear numerous lanceolate and simple hairs of great specific importance.

(5) The mouth-parts consist of a fleshy *labrum*, a pair of small *premandibles*, a pair of long, slender *mandibles* working in the sagittal plane on either side of the labrum, a pair of reduced *maxillae* of fleshy nature with chitinous internal supports, and a simple untoothed *labium*. Within the head there is

a complicated chitinous structure, the *hypopharynx*; this is figured and described in full detail and its action in comminuting the food is revealed for the first time.

(6) No investigation has hitherto been made of the internal anatomy. The *alimentary canal*, consisting of buccal cavity, hypopharynx, oesophagus, mid-gut, and hind-gut, is quite simple in structure, without nodules or caecal chambers. It is only slightly longer than the body, a loop occurring in the hind-gut when the larva contracts.

(7) The *malpighian tubules* are either two or three in number, the latter condition being unique among insects. The third is ventral, passing into the posterior part of the body only.

(8) The *salivary glands* are a pair of S-shaped bodies closely adhering to the walls of the anterior portion of the mid-gut; they are chiefly composed of large binucleate cells.

(9) The *circulatory system* consists of a dorsal vessel extending throughout the body and passing between the lobes of the brain above the oesophagus into the head. In the eighth abdominal segment it enlarges slightly to form the heart, with one pair of ostia or valves situated on its posterior extremity.

(10) The *nephrocytes* are arranged segmentally, four to each abdominal segment and a single mass in the thorax, all attached to the dorsal vessel. The excretory function of these cells was demonstrated by injection of ammonia-carmine into the body cavity.

(11) The *nervous system* is only very slightly cephalised, there being seven ganglia for the eight abdominal segments and three in the thorax; the normal bilobed brain is situated in the thorax in all larval stages. The *sympathetic system* is described, and differs somewhat from that of its close relative, *Chironomus*.

(12) Despite the absence of spiracles there is a well-developed *tracheal system* in the form of two main trunks with transverse connections, branch tracheae, and subcutaneous plexuses.

(13) The *muscular system*, *oenocytes*, *fat-body*, and *gonads* have also been studied in detail.

(14) The larval skin is retained upon the last four or five abdominal segments of the *pupa*.

(15) The characters used for determining the species, in their order of importance, are as follows: *Larva*: chaetotaxy, prothoracic pseudopod, markings of the head, anal blood-gills. *Pupa*: cuticular spines, prothoracic horns.

(16) The larvae and pupae of nine species of *Forcipomyia* are described with particular reference to their specific characters. Descriptions of the adults of two new species, *F. radicicola* and *F. pulchrithorax*, by Mr F. W. Edwards, are appended.

(17) Closely related forms are *Euforcipomyia* and other exotic subgenera not yet named, and the genus *Atrichopogon* (now including *Kempia*). *Dasyhelea*

belongs to this group of hairy-winged flies, but its larvae partly resemble those of the bare-winged Ceratopogonines in that they have lost the prothoracic pseudopod and macrochaetae, but retain the anal hooks.

ACKNOWLEDGEMENTS.

I am greatly indebted to Mr F. W. Edwards of the British Museum for the identification of the many specimens I have submitted to him, and for the descriptions he has prepared of the two new species. He has also lent me material for examination and given me every possible assistance. For the loan of material I also wish to thank Dr M. Goetghebuer, Dr E. Wasmann, Col. W. S. Patton, and Mr R. Butterfield, Curator of the Corporation Museum, Keighley, Yorks. I am extremely grateful to Prof. G. H. F. Nuttall, Director of the Molteno Institute, for the splendid laboratory facilities he has placed at my disposal. Dr D. Keilin, also of this Institute, with his wide knowledge of dipterous larvae, has been an invaluable source of information and encouragement throughout the course of the work.

APPENDIX.

Description of adults of two new species of *Forcipomyia*.

By F. W. EDWARDS, B.A.

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(A) *Forcipomyia radicicola* n.sp.

Head with blackish integument, clothed with short golden hair; orbital bristles long and black. Antennae and palpi black. *Male antennae:* first eight segments of flagellum almost globular, measuring together 115 units; last five segments measuring respectively 15, 70, 30, 20 and 27 units, the two longest segments with nearly globular basal portion and long slender neck; terminal segment rather swollen, with a distinct terminal style. All the hair-whorls transversely, not obliquely placed. *Female antennae* with the first eight flagellar segments one-half longer than the last five together (proportions 27 : 18); each of the first eight flask-shaped, with the terminal portion about half as broad as long and not much shorter than the basal portion; basal hair whorl with about 12 hairs; sense-bristles two in number, pointed, about twice as thick and half as long as the verticil hairs; the part of the segment beyond the sense-bristles with rather numerous short hairs. Last five segments not differing much in shape from the first eight, but more hairy and without sense-bristles; terminal style as in the male. *Palpi* much alike in the two sexes; the long segment slightly expanded on its basal two-thirds, with a small sensory vesicle at the end of the swollen portion; a little longer than the two terminal segments together. *Thorax* with dull blackish-grey integument, clothed dorsally with short golden-brown hairs and longer bristles of the same colour. *Abdomen* black, rather densely covered with black pubescence;

bristles lighter in colour and very numerous. Female lamellae ochreous. *Male hypopygium:* ninth tergite with a pair of rather long and slender terminal processes, placed rather close together; each process with two terminal hairs, the inner longer than the outer. Claspers quite straight, gradually tapering to the tip, with only two or three small bristles. Parameres long, reaching beyond the tip of the side pieces, straight and rather stout on the basal three-fourths, last fourth somewhat sickle-shaped, tip rounded. *Legs* dark brownish, posterior pairs darker, tarsi indistinctly paler; knees ochreous. Proportions of the hind tarsal segments in the male, 12 : 11 : 8 : 5·5 : 5; in female, 15 : 12 : 8 : 5·5 : 5. Female tibiae without scales. *Wings* densely clothed with uniform dark hair, the usual small bare space just beyond the end of the costa appearing like a paler spot. Costa ending just before the middle of the wing, and exactly above the base of the fork of *Cu*. First radial cell obliterated in the male and almost so in the female. Halteres with brownish stem and bright yellow knob. Wing-length, ♂, ♀ 2·3 mm.

Type ♂ and ♀ in the British Museum from Babraham, Cambs., reared from decaying roots of *Arctium lappa*, 2. v. 1919. Other specimens from Letchworth, Herts., reared from roots of *Arctium* and *Pastinaca*, also from Radwell, Herts., from roots of *Angelica*. The first specimens to come under my notice were sent by Mr Eustace Wallis from Kettering, reared from *Angelica* roots. I have also captured adults at Wood Walton Fen, Hunts., and Epping Forest, Essex. The species therefore appears to be common in south-east England, and is probably more widely distributed.

By Kieffer's table of the European species of *Ceratopogon* (*Forcipomyia*) the species will run down to *F. antri-jovis* Kieff., which seems to be closely similar in nearly every respect, but is figured by Kieffer as having only a single minute hair beyond the sense-bristles on the first eight segments of the female antennae, while the sense-bristles are described and figured as being blunt-tipped. If these minute distinctions are really of specific value, better characters will probably be found when the male and larvae of *F. antri-jovis* are discovered; in the meantime, since Kieffer's species has been described only from a single female specimen from Crete, it seems unsafe to assume its identity with the British form.

(B) *Forcipomyia pulchrithorax* (Verrall MS.).

Female. *Head* shining blackish above and behind; front, face, proboscis, and palpi light ochreous. Eyes separated by a narrow line, narrower than the width of one facet. Labium almost as long as the vertical diameter of the head. Second palpal segment with the basal half much swollen on the inner side, about twice as broad as the cylindrical apical half. Last two segments together a little shorter than the second, terminal shorter than the penultimate, shortly oval, all with rather long bristles. Antennae with the scape ochreous, flagellum dark. First flagellar segment nearly globular, second a little longer, segments 3–8 flask-shaped with stout necks slightly and gradually increasing

in length on the successive segments; sense-bristles difficult to observe, apparently rather short and stout. Last five antennal segments about two-thirds as long as the preceding eight together, terminal very little longer than the penultimate, with a short, slender, terminal style. *Thorax* with light yellow-ochreous ground-colour, the mesonotum mainly occupied by three broad, shining, dark brown stripes; the median stripe extends from the front margin to the scutellum and is somewhat broadened posteriorly; the lateral stripes are abbreviated in front, leaving large yellowish shoulder-patches and a yellowish marginal line; anteriorly they are just separate, but posteriorly confluent with the median stripe. Scutellum and the small postnotum black. Pleura almost entirely of the pale ground-colour, the only marking being a small dark brown spot below the base of the wing. Mesonotal and scutellar bristles not very dense, all dark brown, long and short ones regularly mixed. *Abdomen:* the membranous parts pale ochreous, tergites dark brown with rather short black pubescence, separated at the normal distension by conspicuous strips of membrane. Sternites light brown, undivided. Last segment with very long, dark bristles. Lamellae pale, nearly circular. *Legs* uniformly pale ochreous, the hind femora darkened at the tips. All tibiae on the outer surface with a few dark scales (only two or three on the front tibiae), which are shortly petiolate and somewhat rounded at the tips. Vestiture all pale. Second tarsal segment on the fore and mid legs a little longer than the first, on the hind legs about 1·6 times as long as the first. Empodia well developed. *Wings* densely clothed with dark hair; the base and a small but distinct spot on the radial cell yellowish. First radial cell entirely obliterated by the fusion of *Rs* with R_1; second radial cell of the usual shape for the genus, about half as long again as broad. Costa barely reaching the middle of the wing; cubital fork immediately below the end of the costa. Halteres yellow, the stem slightly darker than the knob.

Male. Second palpal segment rather less swollen than in the ♀. Antennal plumes black, except at the tip, which is whitish. Scape dark brown. First nine flagellar segments nearly globular, with short necks; last four segments much as figured by Goetghebuer for *F. ciliata* Winn. (as *C. boleti* Kieff.), but the terminal style a little longer and more slender. Mesonotum with the humeral spots distinct, but smaller than in the ♀, the dark stripes broader and touching the margins. Pleurae extensively dark brown. Claspers straight, the basal three-fifths somewhat enlarged on the outer side; extreme tip turned inwards. Femora and tibiae extensively but not strongly darkened on the mid and hind legs. Second tarsal segments somewhat longer (relatively to the first) than in the ♀.

Length of body, 1·8–2·0 mm.; wing, 1·3 mm.

The British Museum possesses the following cotypical material: 2 ♂, 2 ♀, "bred from (material with) *Xylomia pabulum*, New Forest, vi. 1905" (G. H. Verrall); 1 ♂, 1 ♀ "bred from wood debris, Snailwell, Cambs., vi. 1906" (G. H. Verrall); 1 ♂, 2 ♀ "from larvae living in sap flowing from wound in elm,

Cambridge (corner of Garret Hostel Lane on Backs), ix. 1919" (D. Keilin); 1♀ "from larvae found in running sap of chestnut tree, Cambridge (by new Biochemistry Building), ix. 1922" (L. G. Saunders).

This species is very distinct from all those of the genus at present known from Europe by the coloration of the thorax. It belongs to the small group of species which have long scales on the female tibiae. The specific name was proposed by the late Mr G. H. Verrall, though never actually published by him.

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EXPLANATION OF PLATES X—XII.

PLATE X.

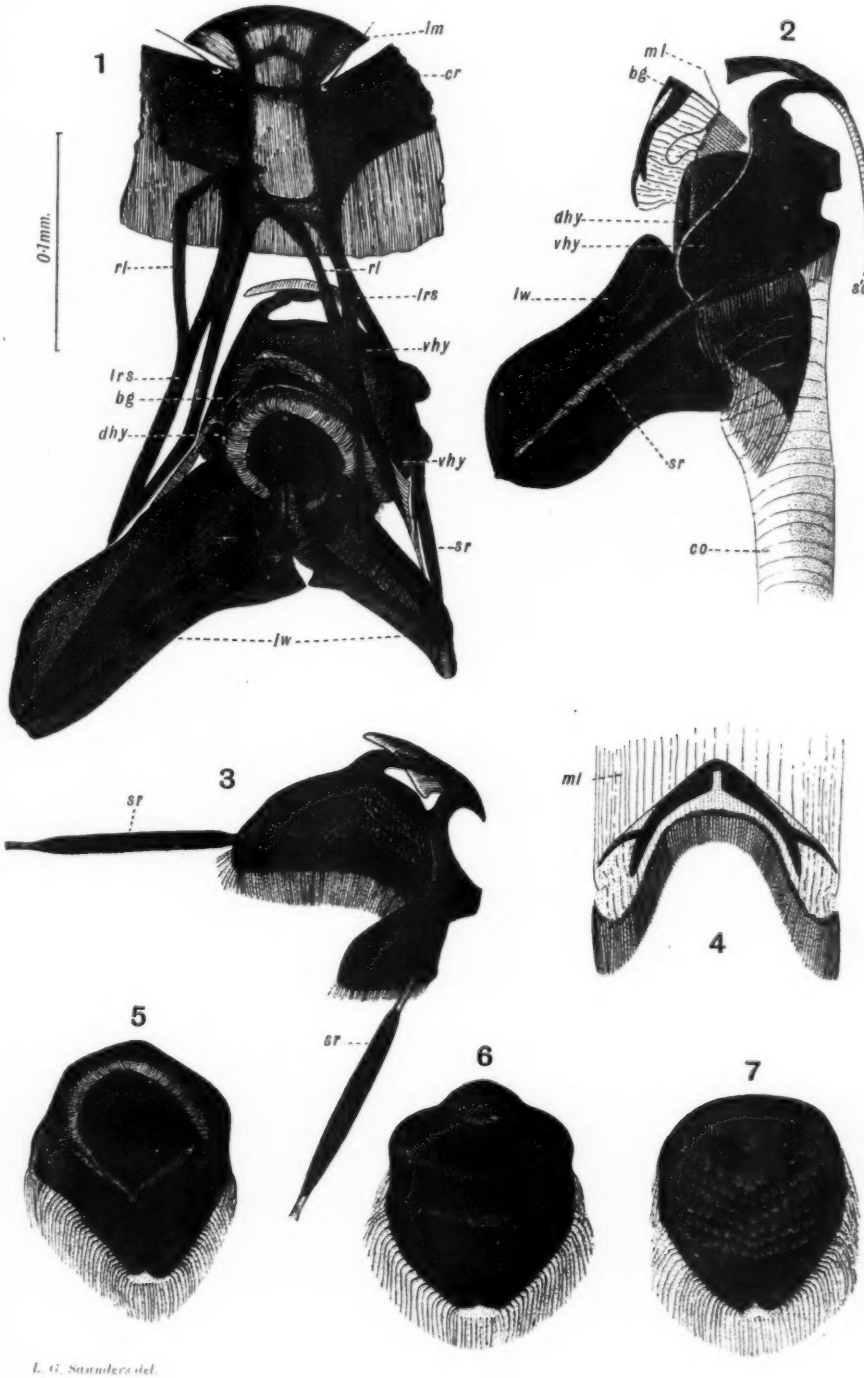
THE HYPOPHARYNX[1].

(All figures except 7 refer to *F. bipunctata*.)

Fig. 1. The entire apparatus, dorsal view; most of the head capsule has been removed.

Fig. 2. Lateral view; the lateral rod systems have been removed, and only the left half of the bridge is figured.

[1] See p. 174.



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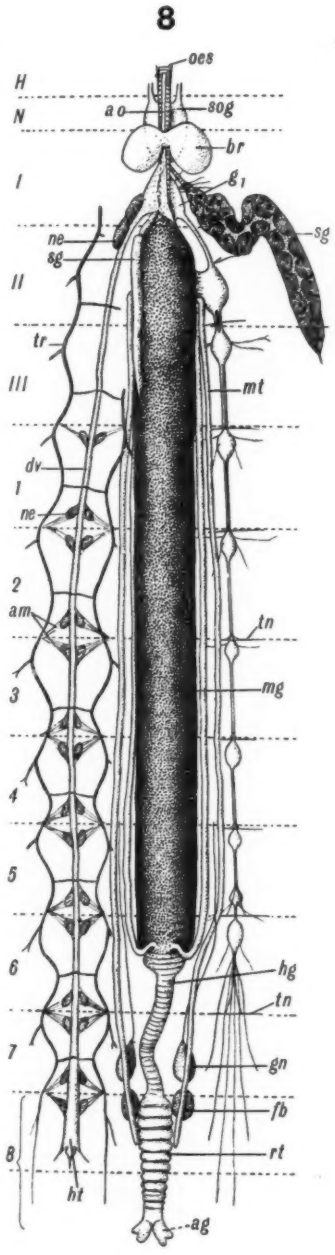

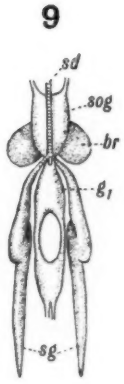

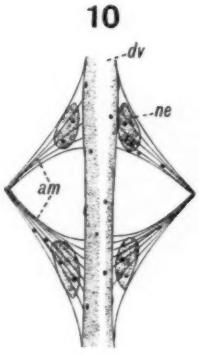

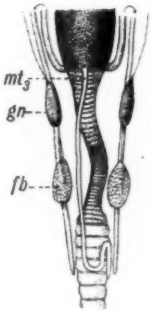

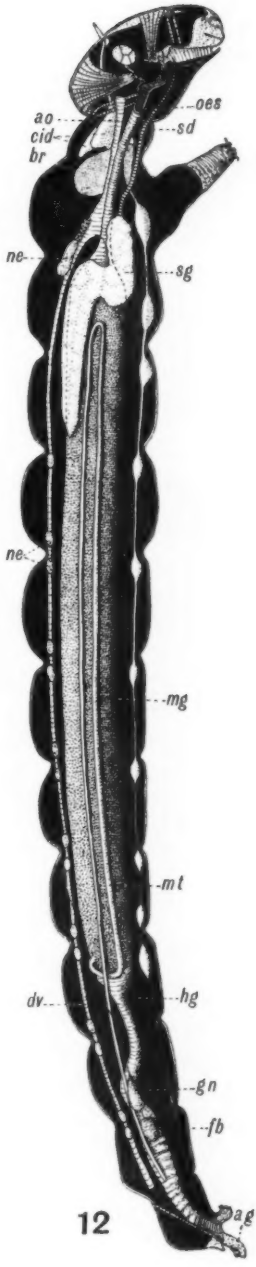

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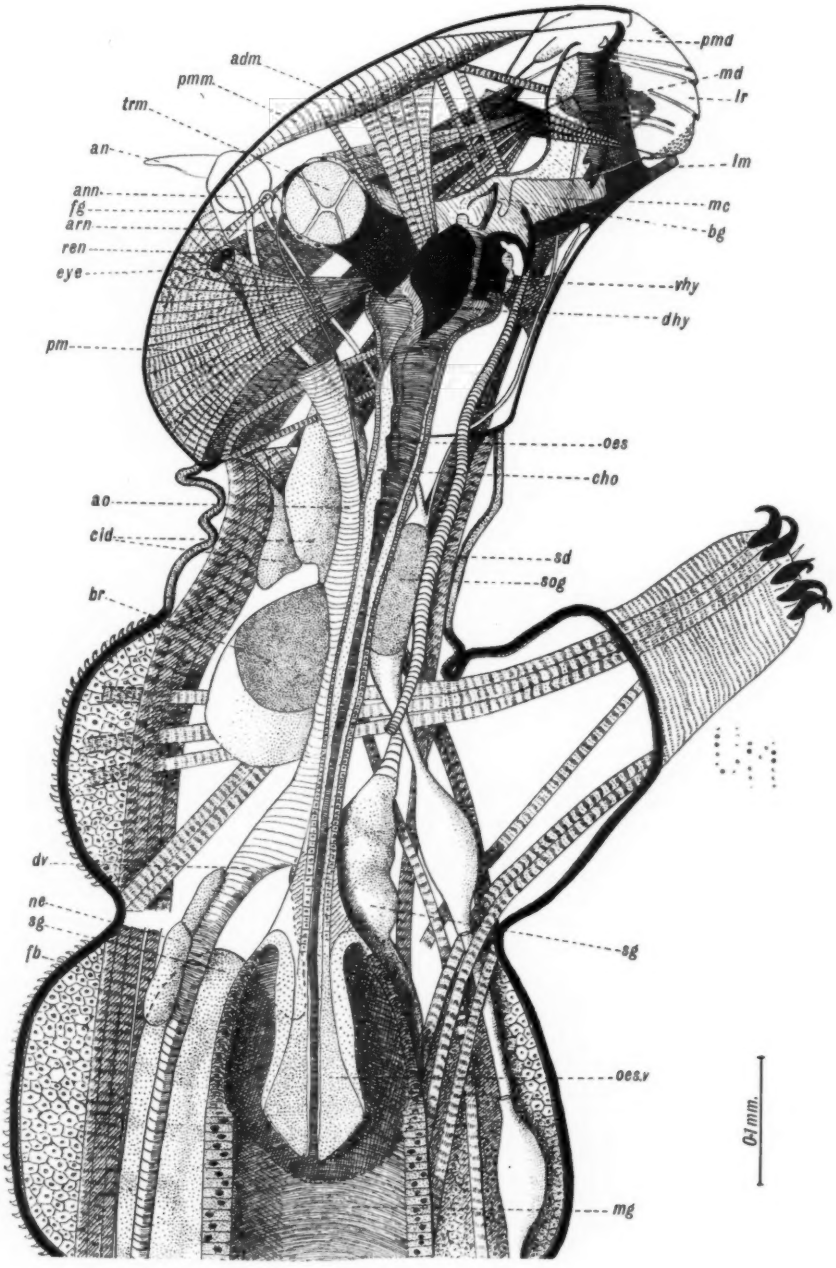

L. G. Saunders del.

Fig. 3. The ventral portion, with its suspending rods, dorsal view.
Fig. 4. Postero-dorsal view of bridge.
Fig. 5. Antero-dorsal view of the central sclerite of the dorsal portion.
Fig. 6. Ventral view of the central sclerite of the dorsal portion.
Fig. 7. Ventral view of the central sclerite of the dorsal portion, *F. picea*.
(The scale of magnification refers to all figures except 4.)

PLATE XI.

(All figures except 11 refer to *F. bipunctata*.)

Fig. 8. General dissection of the internal anatomy viewed dorsally. The ventral nerve chain is displaced to the right, the dorsal vessel and tracheae to the left; the right salivary gland is displaced and its cellular structure indicated, the left remains *in situ*.
Fig. 9. Ventral view of the anterior portion of the nervous system and salivary glands.
Fig. 10. Enlarged portion of the dorsal vessel with alary muscles and nephrocytes.
Fig. 11. Ventral view of hind-gut of *F. picea* to show the third malpighian tubule.
Fig. 12. Lateral optical section of an entire larva to show the natural position of the internal organs.

PLATE XII.

Lateral optical section of the head and first two thoracic segments of a larva of *F. bipunctata*.

KEY TO LETTERING OF PLATES.

ao, Aorta.
ag, Anal blood-gills.
adm, Anterior dorsal muscle of hypopharynx.
am, Alary muscle.
an, Antenna.
arn, Arched nerve.
bg, Bridge of hypopharynx.
br, Brain.
cho, Chitinous intima of oesophagus.
cid, Cephalic imaginal disc.
cr, Chitinous ring of head capsule around mouth.
dhy, Dorsal portion of hypopharynx.
dv, Dorsal vessel.
eye, Eye.
fb, Fat body.
g_1, First thoracic ganglion.
gn, Gonad.
H, Head.
hg, Hind-gut.
ht, Heart.
lm, Labium.
lr, Labrum.
lrs, Lateral rod system.
lw, Lateral wing of hypopharynx.
mc, Mouth cavity.
md, Mandible.
mg, Mid-gut.
ml, Membrane which forms the lower surface of the labrum.
mt, Malpighian tubule.
mt_3, 3rd Malpighian tubule.
N, Neck.
ne, Nephrocyte.
oes, Oesophagus.
oesv, Oesophageal valve.
pm, Posterior dorsal muscle of hypopharynx.
pmd, Premandible.
pmm, Muscle operating premandible.
ren, Recurrent nerve.
rl, Rod passing into posterior part of labrum.
rt, Rectum.
sd, Salivary duct.
sg, Salivary gland.
sog, Suboesophageal ganglion.
sr, Suspensory rods of hypopharynx.
tn, Transverse nerve.
tr, Tracheal trunk.
trm, Transverse muscle connecting lateral wings of hypopharynx (in cross section).
vhy, Ventral portion of hypopharynx.
I, *II*, *III*, Three thoracic segments.
1–8, Eight abdominal segments.

(*MS. received for publication* 7. XII. 1923.—Ed.)

BIOGRAPHICAL NOTES BEARING ON KOCH, EHRLICH, BEHRING AND LOEFFLER, WITH THEIR PORTRAITS AND LETTERS FROM THREE OF THEM.

By GEORGE H. F. NUTTALL, F.R.S.

(With Portrait-plates 26–29, two Letters and a Signature in facsimile.)

(*From the Molteno Institute for Research in Parasitology, University of Cambridge.*)

[Continuing the Series begun in *Parasitology*, vol. XIII, p. 398.]

The four distinguished German men of science to whom the following biographical notes relate: Robert Koch (1843–1910), Paul Ehrlich (1854–1915), Emil von Behring (1854–1917), and Friedrich Loeffler (1852–1915), form a group of singular interest because of the relations that existed between them and the various problems to the solution of which they devoted their remarkable talents and energies. Each of them has left an indelible mark upon the annals of research and discovery in relation to infective diseases of man and animals, their etiology, prevention and cure. If it were at all possible to reckon up the sum of human and animal lives that they have saved from premature extinction through their collective efforts, direct and indirect, the total would attain gigantic proportions. Mankind should ever keep these men in grateful memory.

Having had the privilege of knowing them individually, von Behring unfortunately but slightly, it seemed expedient to write of them at greater length than has been done of the subjects of earlier biographies published in this journal. Recently, in looking through old letters, I found three which I now value greatly as mementoes and which seem to me worthy of publication because of what they contain as records and expressions of the character of the several writers.

Robert Koch.

1843–1910.

(Portrait-plate 26 and Facsimile of Letter.)

Robert Koch was born on the 11th of December, 1843, at Clausthal. He was the third child in a family of thirteen, eleven sons and two daughters; two of his brothers died in infancy. The father of this large family was an active and efficient Hanoverian mining official. In 1862, on leaving the Gymnasium,

Robert proceeded to Göttingen to study mathematics, physics and botany, but he soon became a student of medicine and, in his seventh semester, became Assistant at the Pathological Museum under Henle. He took his M.D. in January, 1866. On leaving Göttingen he sojourned for a short time at the Hamburg General Hospital and also near Hanover, after which he established himself, in 1869, in practice at Rakwitz in Posen. He served as a physician during the Franco-Prussian War (1870–1) and in 1872 moved to the little town of Wollstein in the District of Bomst, Polish Prussia, where he became District Physician. Whilst busily engaged in practice, he began to study the subject of anthrax upon which he was destined to throw a flood of light by his researches. His laboratory consisted merely of a curtained-off portion of a large room in which he worked and received his patients. He provided himself with a good microscope and arranged by simple means a photographic room on the premises.

Whilst Koch was working on unaided, the study of microorganisms was being actively pursued by Ferdinand Cohn, Professor of Botany, at Breslau. Cohn's studies had convinced him of the existence of different species of microorganisms and that it was necessary to devise means for their isolation in pure culture. Cohn had discovered certain bacilli which formed spores and actually foretold that the *Bacillus anthracis* would prove to be sporogenous. Cohn was therefore much gratified when he received a letter from Wollstein, dated 22 April, 1876, in which the young physician, Robert Koch, reported that he had made a biological study of the anthrax bacillus and found that it produced spores as Cohn had surmised. The latter immediately invited Koch to visit him and gave Koch the opportunity of demonstrating his specimens and methods to others at the Botanical Institute. Koch's evidence was complete, tracing as it did successively the development of the spores in the bacilli, their liberation, and the sprouting of bacilli from spores. The life-cycle of the bacillus when cultivated in blood serum or aqueous humor was thus demonstrated. Spore-formation was shown to occur in shed anthracic blood and Koch transmitted anthrax by inoculation to mice, rabbits, etc., by the inoculation of anthrax bacilli or their spores. These results threw light into the hitherto obscure etiology of anthrax. Koch's demonstrations greatly impressed his hearers (Cohnheim, Weigert, Traube, and others) and the importance of his discovery made his name known throughout the medical world. His classical researches on anthrax were published in July, 1876, in Cohn's *Beiträge zur Biologie der Pflanzen*; they afforded the first clear demonstration of the causal relationship between a specific microorganism and a specific disease, for it was the first occasion on which a pathogenic organism had been cultivated and the disease reproduced by means of pure cultures. The results obtained by Koch were subsequently confirmed by Pasteur and others.

In 1877 Koch described how coverglass *preparations of bacteria* are made by smearing the substance to be examined upon the glass in a thin layer,

fixing it by the heat of a flame and staining the film by aniline dyes. He showed how the flagella of bacteria could be stained and how microorganisms could be photographed. *Photomicrographs* published by Koch in 1881 have scarcely been surpassed to this day and it must always be remembered that he worked as a pioneer with the simplest of means.

In 1878 he published his researches on the etiology of wound infections and described various improvements in methods including the use of oil-immersion objectives and sub-stage condensers for bacteriological investigation.

In 1880 he was called to the Imperial Health Department, Berlin, where he worked with great diligence and success upon the problems of *disinfection*. His investigations placed the subject upon a scientific basis. He introduced steam-sterilization into practice and taught how this and chemical disinfectants should be applied in accordance with the results of bacteriological tests. The methods laid down by Koch have not undergone any material change because of their fundamental character. Koch was aided in these researches by his pupils Gaffky and Loeffler.

The need of devising *means whereby microorganisms could be readily isolated*, had occupied Koch from the time he first attacked the problem of anthrax. After trying various procedures he bethought himself of adding gelatin, and later agar, to the nutrient fluid medium, thereby discovering a simple manner of overcoming the difficulty. Koch was the first to use solidifying media for the cultivation of microorganisms, and his method has been employed ever since by bacteriologists and others. When Koch demonstrated his method to Pasteur at the International Congress of Medicine held in London in 1881, the great Frenchman exclaimed: "Ah, voilà, c'est un très grand progrès." Up to within a year of his death Koch regarded his discovery of the use of solid media and his methods of bacteriological research as constituting his most valuable contribution to science. There are many who will agree with him having regard to the great results that have followed the employment of Koch's methods by scientific workers throughout the world.

At a memorable meeting of the Berlin Physiological Society, held on 24 March, 1882, Koch announced his discovery of the *Bacillus tuberculosis*. He described a special method for staining the bacillus and of cultivating it upon solidified blood-serum. He demonstrated that tuberculosis could be produced in certain laboratory animals by inoculation with pure cultures of the bacillus. Ehrlich, who was present at the meeting, relates how all who heard Koch speak on that occasion were greatly moved. Ehrlich himself, in 1910, recalls the events of that evening as having afforded him his "greatest scientific experience." Koch spoke in clear and simple language and demonstrated innumerable specimens in a most convincing manner.

To appreciate the full import of Koch's discovery of the tubercle bacillus, we must recognize that he approached the study of the etiology of tuberculosis in a manner contrary to the views of Virchow, which then held the field. Although tuberculosis was recognized as having many forms, Koch regarded

these as all attributable to but one cause, a specific agent that remained to be discovered. He was confirmed in this opinion by experiments of Cohnheim and Salomonsen, wherein tuberculosis of the iris was induced experimentally in rabbits by inoculation, no one at the time having any conception as to the nature of the virus. Koch, as the result of unremitting toil, solved the problem in six months and in such a masterly manner that his name grew famous throughout the world. His discovery will ever stand as a landmark in the history of medicine and the way in which he presented his evidence may well serve as a model for all time.

In 1883 Koch proceeded to Egypt and thence to India to study *cholera*. In Calcutta he confirmed and extended observations begun in Egypt, and was able to announce the discovery of the cholera vibrio as the cause of this dread disease, thereby affording effective means for combating the scourge successfully.

In 1885 Koch was called to the newly-founded *Professorship of Hygiene* at Berlin and, in November, began to lecture at the Hygienic Institute that was established at 36 Klosterstrasse. Students flocked to him from all quarters of the globe and he quickly gathered about him a school of bacteriologists, many of whose members subsequently attained high distinction. Among those associated with him were R. Pfeiffer, M. Kirchner, C. Fraenkel, L. Brieger, G. Gaffky, etc. The Institute was so crowded that when I applied to Koch for admission as a research worker in the autumn of 1886, it was impossible to find a place. Koch received me very amiably but pointed out the crowded heads of men bending over work-benches, seen through the windows across the Court, and advised me to seek more commodious quarters in Carl Flügge's Institute at Göttingen.

An immense amount of work was being turned out of the Institute by Koch and his disciples[1]. After trying in vain to check or ameliorate tuberculosis in animals by chemical agents, Koch made an observation of fundamental importance, namely, that tuberculous guinea-pigs react differently to healthy guinea-pigs when inoculated with living or dead tubercle bacilli. He followed up this clue, reasoning that the tubercle bacillus should give off a soluble substance which would serve as a remedy and means of diagnosis. This substance, which he subsequently found, was prepared as a glycerin extract of pure cultures of the tubercle bacillus. The discovery of the substance, afterwards called *tuberculin*, was announced as a cure for tuberculosis at the International Congress of Medicine, held in Berlin in 1890. Expectations were raised to a high pitch throughout the world owing perhaps to Koch's insufficiently guarded statements as to its efficacy, but chiefly owing to the gross exaggeration of journalists and uncritical medical men. The inevitable result followed in that Koch and his methods became subject to much unwarranted disparagement. The continued use of tuberculin to this day, in the treatment of well-selected cases and in diagnosis, have largely disposed of

[1] See Loeffler's tribute to Koch's stimulating effect on those about him, p. 235.

hasty judgments that were generated by the storm of adverse opinion in which people so commonly follow each other's lead. Subsequently Koch sought to improve upon the original tuberculin, by making a preparation consisting of ground-up tubercle bacilli, but this proved on the whole less efficient than the original tuberculin. The use of tuberculin as a remedial agent constitutes the first attempt at vaccine therapy.

In 1891 Koch, having given up teaching, became the first Director of the newly-founded *Institute for Infective Diseases*. He held this post until 1904, when he was succeeded by Gaffky. Beginning with the year 1896, Koch became engaged in researches which took him abroad, this doubtless being attributable to his disappointment over the reception accorded to his tuberculin as a remedy, coupled with the attitude adopted by society consequent upon his separation from his wife and his second marriage.

In 1896, therefore, at the age of fifty-three, with the best of his life's work accomplished, but brimful of interest in new problems, he left for South Africa, where, at Cape Colony, he proceeded to investigate *rinderpest*. As a method of preventive inoculation he advocated the use of affected animals' bile, a mode of treatment long practised by the natives, and in addition made initial experiments upon the serum therapy of the disease. Thence he proceeded to Bombay as head of the *German Plague Commission*. At this time he was responsible for an edict issued by the German Government forbidding all research work on plague within the precincts of German laboratories. I was then carrying out flea-transmission experiments with plague which, consequent upon this order, had to be suspended. In 1897 he returned to Berlin and the following year found him working on *malaria* in Rome. His researches on malaria were mainly confirmatory of the fundamental work of Ross, and of MacCallum's observations. Anti-malaria measures advocated by him in German East Africa and New Guinea (1899–1900) led to a reduction in malaria-incidence in those countries.

At the International Congress on Tuberculosis held in London in 1901, Koch's pronouncement regarding the *relation between bovine and human tuberculosis* came as a shock to the medical and veterinary professions of the world, running counter as it did to established hygienic measures designed to prevent the infection of man through the agency of tubercular cattle and cows' milk. A measure of justification for Koch's dictum may be found in the circumstance that bovine tuberculosis is relatively speaking infrequently communicated to man, but the attitude of the professions named has nevertheless remained to this day in opposition to Koch's views. This does not militate against Koch's further assertion that man finds in man the chief source of tubercular infection. Koch's attitude on the subject did good service since it led directly to the appointment of a second British Royal Commission for the investigation of the problem.

In 1902 we find Koch working on *Rhodesian or East Coast Fever and Piroplasmosis* (Redwater) of cattle in Africa. In 1903 he celebrated his

sixtieth birthday at Bulawayo. In 1906 he headed the German Expedition sent out to study *Sleeping Sickness* in German East Africa and British Central Africa. Here he employed atoxyl in the treatment of the disease and devised the method of clearing the foreshore of Lake Victoria Nyanza to eradicate *Glossina palpalis* by attacking its breeding grounds.

In 1908 Koch visited his brothers in the United States and, likewise for pleasure, journeyed to Japan, returning thence to Washington to attend a Congress at the instance of his Government. Finally, he returned to Germany to again take up his work on tuberculosis.

For some years prior to his death Koch was occasionally subject to circulatory disturbances, but he nevertheless continued to work uninterruptedly. My late friend Professor Carl Fraenkel, a distinguished pupil of Koch's, recounts how he witnessed Koch's suffering from a heart-attack whilst with him in Japan and how Koch felt his own pulse when he thought himself unobserved. Koch was therefore perfectly aware of his own condition but he worked on persistently. In March, 1910, severer heart-symptoms occurred that were accompanied by dyspnoea and pain in the cardiac region. In April he had a sudden attack of heart weakness with oedema of the lungs from which, however, he rallied sufficiently to travel to Baden Baden comfortably, but eight days after his arrival, nearly at the age of 67, on May 27th, Koch breathed his last peacefully. Three days later, in accordance with his wishes, his remains were cremated at Baden Baden.

Robert Koch was a man characterized by fearlessness, clear and quick insight, good critical judgment, dogged perseverance and great working capacity. His pupils, with whom he stood on an intimate footing, all agreed in stating that he spoke freely with them and was exceptionally amiable and modest, never striving for popularity with the masses, and that his mind was mainly concentrated upon the advancement of science for the benefit of mankind. In his last years, when among intimates, he liked to tell of his varied experiences abroad, and he astonished many by his broad knowledge, especially of botany and zoology. He moreover sought distraction in other sciences, occupying himself for pleasure with such very different subjects as mathematics, physics, chemistry, astronomy, geology, anthropology and ethnology, the last especially during his travels abroad. With strangers, as a rule, he was reserved and a man of few words. Personally I found him most amiable on the occasions when I met him[1]. He was generally acknowledged not to be a graceful speaker.

[1] The last occasion upon which Koch received me in his room at the Institute was in the winter of 1895, when I fell under the spell of his personality. This was not altogether due to our conversation drifting to the subject of immunity and his referring to my researches on the bactericidal properties of blood (*Zeitschr. f. Hygiene*, vol. IV. 1888), of which he spoke as having been "the foundation of the late advances usually spoken of as serum therapy." This recognition, coming from Koch in whose laboratory Behring made his discovery of antitoxic sera, could not but be specially valued by me since Koch knew all the circumstances under which the work had been carried out.

He spoke simply and to the point in a manner that did not fail to impress his hearers.

In Germany Koch's activities were not confined to research and teaching. He was constantly called upon by his Government in an advisory capacity. In 1886, in conjunction with Flügge, he founded the *Zeitschrift für Hygiene*, a journal of high scientific standing which is still appearing.

Many felt that the weight of Koch's authority in his domain was at times too great, especially in its influence on Government, and, unless Koch expressed a favourable opinion of a discovery, it was liable to be received with doubt by German men of science. Moreover, when Koch or members of his school had been given the opportunity of confirming the work of others, there was a decided tendency to arrogate to themselves undue credit in discovery. This resulted in ill-feeling that was none the less bitter because it did not always find its way into print. Men feared to stand up against Koch because they felt his influence, if directed against them, might injure them in their career or lead to the loss of a coveted post. Under the circumstances, Koch was in a position to push others aside and on occasion he did so. Thus, to my knowledge, when an obscure but observing young veterinarian in German East Africa had found *Piroplasma bigeminum* in cattle suffering from redwater and had shown the parasites to Koch, we only heard of Koch's work thereon afterwards. When Metchnikoff brought malaria blood-films from Russia in 1887, and demonstrated these to Koch, he was treated, as he told me himself, with scant courtesy, for Koch apparently still disbelieved in the existence of the malaria parasites that Laveran had discovered in 1880; at any rate Koch denied that Metchnikoff's slides showed malaria parasites. The latter had, however, demonstrated his excellent preparations to Professor Flügge and to me some days previously in Breslau and we had seen the parasites. This experience certainly hastened Metchnikoff's journey on to Paris. Furthermore, when Grassi, Bignami and Bastianelli in Rome, stimulated and directly guided by the epoch-making discoveries of Ronald Ross on malaria, confirmed and extended the latter's work, the antagonistic attitude adopted by Koch was extreme. It was therefore generally held in Berlin that the work of the Italian observers was worthless, and it was not until I demonstrated some of Grassi's specimens in Berlin, after having gone to Rome (March 1st, 1899) to fetch them, that a measure of credence was given by some authorities in Germany to the reported results of the Italian researches[1].

[1] It must be assumed that Koch did not see any of the preparations made by Grassi and his colleagues, for so late as 10th February, 1901, close on two years after I visited Grassi, Koch wrote to Ross (vide *Memoirs* by Ronald Ross, London, 1923, p. 409) of Grassi's work: "His statements regarding the development of the malaria parasites in the mosquito's body, if really observed by him as described (which I do not believe), are but a confirmation of your discoveries. His illustrations are direct copies of yours" (my translation). Whilst agreeing that Grassi's claims to original discovery deserve some of the criticism they have received, it is but fair to separate the good from the bad and to give him and his colleagues their due. When in Rome, I compared the Italian authors' figures with their specimens and found them to agree. I still possess some of these specimens and it cannot be asserted that they are the products of Grassi's imagination.

Although it is unpleasant to dwell on this aspect of Koch's character I have felt it incumbent upon myself to do so with a view to giving a true picture of the man, not as he might have been but as he was. The instances I have cited might be multiplied, but they will suffice to show that, great as he was, Koch had his weaknesses. I presume that constant appeals to him for his opinion may have adversely affected his judgment on some matters, in which case there are obvious disadvantages in being too great an authority in the eyes of one's fellow-men.

To recapitulate briefly, Koch's work was fundamental in respect to the methods to be pursued in bacteriological investigation; we have to thank him still for many every-day methods that are employed in laboratories, hospitals, preventive medicine and public health. He threw light upon the etiology of anthrax, discovered the cause of tuberculosis and cholera, thereby placing in our hands the means of diagnosis and indicating how these diseases may be combated. By a careful study of the processes of water-filtration he laid down principles for the prevention of water-borne diseases like cholera and typhoid. His thorough and methodical work upon the theory and practice of disinfection by heat and by chemicals still serves us as a guide. His contributions to tropical medicine and parasitology, especially in relation to East Coast Fever in cattle, Malaria, and Sleeping Sickness were important.

Research upon Immunity, which was pursued by purely empirical methods before the advent of Pasteur, attained a great impetus in bacteriological laboratories through the influence of Koch and his methods. Bacteriotherapy, now so much in vogue largely through the efforts of Almroth Wright, may be regarded as having had its birth in the discovery of Koch's tuberculin as a remedial agent. It was in Koch's laboratory that Behring discovered the first antitoxin, and that Pfeiffer discovered bacteriolysins. It was Koch who first advocated the systematic use of quinine in combating malaria, for he conceived that this disease could be eradicated by discovering the infected persons in a community and subjecting them to radical treatment, thereby ridding

When two observers illustrate what amounts to the same thing, it is to be expected that their figures will closely correspond. Ross's figures were those drawn by a pioneer working single-handed under great difficulties whilst seeking out fundamentals, those of the Italians were the products of a European laboratory with a technically-trained staff. By good sections, excellent staining technique and an artist's help, this staff naturally produced specimens and illustrations which greatly surpassed those of Ross and consequently appealed more strongly to zoologists, though they established no principles other than those laid down or indicated by the work of Ross.

It is clear that full credit must be given to Grassi and his colleagues for having been the first to demonstrate that the human malaria parasites have a cycle of development in *Anopheles* corresponding exactly to that demonstrated by Ross for *Proteosoma* in *Culex*. On the other hand there can be no question but that Ross observed the early stages of the development of one species of human malaria parasite (*praecox*) in *Anopheles*. Unfortunately, for reasons which are fully explained in his *Memoirs*, Ross was unable to do more than to predict that the immature forms ("pigmented cells," 1897) observed by him in *Anopheles* would complete their development as in *Proteosoma*. For a full discussion of this subject, see Nuttall (1902), "On the Question of Priority with Regard to certain Discoveries upon the Ætiology of Malarial Diseases," *Quarterly Journal of Microscopical Science*, n.s. vol. XLIV. pp. 429–441.

them of parasites and rendering them no longer capable of infecting the anopheline vectors. He moreover introduced atoxyl in the treatment of Sleeping Sickness in Africa.

The value of the services Koch rendered to his country and mankind throughout the world led to his having the title of Excellency conferred upon him by the German Emperor in 1907, but he was not granted the patent of nobility, doubtless owing to his domestic relations. He was awarded the Nobel Prize in 1905, and was the recipient of many honours from learned societies and universities, besides decorations of which may be mentioned the rare Ordre pour le Mérite conferred upon him by his Sovereign. The Institut für Infektionskrankheiten "Robert Koch" remains as a visible memorial of him. Koch, through the magnitude of his services to mankind, will ever be kept in grateful memory. In the annals of medicine his name should be enrolled with the immortals.

The accompanying portrait of Robert Koch dates from about the year 1907, some three years before his death.

See facsimile[1] *of a letter by Robert Koch to G. H. F. Nuttall on opposite page.*

Translation:

The thought that mosquitoes play an important part, possibly the whole part in the etiology of malaria, came to me during my first sojourn in India in 1883–4, when for the first time I learnt to know the conditions: under which tropical malaria flourishes and highly malarious regions; since then I have always expressed myself in this sense, especially in my lectures and courses. Naturally, I have not referred to this until recently, but R. Pfeiffer mentions it in his *Beiträge zur Protozoenforschung*, Berlin, 1892, p. 22.

REFERENCES.

In writing the foregoing biography I have made free use of publications that were kindly sent to me in reprint form in 1910, shortly after their appearance, by Professors Carl Fraenkel (*München. med. Wochenschr.* p. 1345), P. Uhlenhuth (*Med. Klinik*, No. 24), G. Gaffky (Gedächtnisrede in *Deutsche med. Wochenschr.* No. 50), and subsequently by Dr W. W. Ford (*Johns Hopkins Hosp. Bulletin*, 1911, vol. XXII. p. 415, giving list of chief publications) and Prof. W. Kolle (*Med. Klinik*, 1913, Nos. 51–2). See also C. J. Martin (*Brit. Med. Journ.* 1910, vol. I. p. 1386, and editorial on p. 1384) and P. Ehrlich (*Zeitschr. f. Immunitätsforsch. u. exper. Therap.* 1910, Orig., vol. VI. part 1). W. Becher (1891), *Robert Koch, Eine biographische Studie*, may be consulted, likewise Koch's earlier publications issued (1886) in English translation by The New Sydenham Society.

[1] Reduction by 1/5.

ROBERT KOCH

1843—1910

Berlin N. W. Charitéstr. 1.
d. 14. Nov. 1898.

Sehr geehrter Herr Kollege!

Vor Jahren, dass die Anschauungen in der Klinik, für die Malaria eine specifische, ursächliche Rolle spielen, Ihnen mir bei meinem ersten Aufenthalt in Indien 1883/84, also in der ersten Zeit die Verschiedenheit zwischen der tropischen Malaria und gewöhnlichen Wechselfieber klar. Seitdem habe ich mich immer in diesem Sinne, namentlich auch in meinen Vorlesungen und Büchern ausgesprochen. Vollst. gründlichst habe ich durch die Arbeiten derselben, sowie R. Pfeiffer

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vervollständigt in seinem: Beiträgen zur Protozoenforschung Berlin 1892. p. 22.

Hochachtungsvoll

R. Koch

Paul Ehrlich.

1854–1915.

(Portrait-plate 27.)

PAUL EHRLICH was born on the 14th of March, 1854, at Strehlen in Silesia. After leaving the Maria-Magdalena Gymnasium in Breslau, he went as a University student to Breslau, Strassburg, Freiburg and Leipzig successively. He took his M.D. in Strassburg in 1878. He was influenced by the teachings of Waldeyer, Heidenhain and Cohnheim and at an early date showed his aptitude for research. Whilst still a student he devoted himself to the study of the *histology of the blood*. In Breslau (1877), before he became professionally qualified, he was struck by the existence of a chemical affinity between certain organs and chemical poisons as instanced in the case of lead; this served as a basis upon which he subsequently built up his theory of *selective anchoring* which was grounded on the belief of the existence of chemical affinity between certain tissue cells and a particular poison. This conception dominated his viewpoint to the end of his life. His work on blood led to his becoming interested in *aniline dyes* this interest being especially stimulated through his cordial relations with his cousin Karl Weigert.

In 1878–85 he was stationed at the Charité Hospital in Berlin as assistant under Frerichs. Here he worked out methods of blood diagnosis and of colour analysis, upon the diazo-reaction (1883), on the affinity possessed by methylene-blue for living nervous tissue-elements, upon specific staining reactions of the tubercle bacillus and its acid-fastness (1882). In 1885–7 he was assistant to Gerhardt and during this period he published his monograph, *Das Sauerstoff-bedürfniss des Organismus* (1885), which embodied the results of his researches. This contribution already outlines the principles upon which he based his famous "side-chain theory" that he evolved many years later; this work still affords stimulating reading. In 1888 Ehrlich suffered from what appeared to be but an obstinate catarrh, but on examining his sputum he found it to contain tubercle bacilli. He therefore went to Egypt, underwent a course of treatment with Koch's tuberculin, and, having recovered from his symptoms, returned to Berlin to pursue his researches. He became Privatdocent in 1889, and in 1890 received the title of Professor also being made Mitarbeiter at the Institute for Infective Diseases. He at first worked on tuberculosis in association with Koch and afterwards alone on the subject of *immunity in relation to vegetable poisons* (ricin, abrin and robin), finding that he could immunize animals against these poisons, corresponding antitoxins being formed in their blood; these antitoxins, being eliminated in the milk of immunized animals, served to immunize their offspring.

Ehrlich now attacked the fundamental problems of immunity and *serum therapy*. Guided by his experience in immunizing animals against the poisons of higher plants, above mentioned, and having regard to Behring's discovery of the antitoxins for bacterial poisons, he worked methodically upon the

production of *diphtheria antitoxin*, thereby furnishing a curative serum that could be used in medical practice. Considered scientifically, this was of subsidiary importance. The chief credit that lay in Ehrlich's work at this period was his introduction of *quantitative methods* into work on immunity problems, in his distinguishing *active* from *passive immunity* (he established this terminology), and applying his experience as a chemist to the problem of evolving methods whereby the potency of toxins and antitoxins could be tested. This work of Ehrlich's (1896) gave us the methods that are being used to the present day.

In 1896 he was placed at the head of the newly-founded *Institute for Serum Testing and Serum Research at Steglitz*, near Berlin. It was a joy to him to be in a laboratory of his own where he could work on independently. To those of us who knew the circumstances under which he laboured at Koch's Institute it was common knowledge that his freedom in carrying on research was being interfered with. Soon after he had established himself in his new quarters, I sought him there and found him in the company of L. Brieger. It was touching to see his delight in at last finding himself complete master of his own actions. His work at Steglitz, pursued with enormous energy, led to the exposition of his *side-chain theory*, according to which the effect of a toxin on a particular organ is due to the cells of that organ containing substances ("receptors") having a special affinity for the toxin. Owing to this affinity the toxin becomes fixed in the particular organ. The antitoxins are merely receptors, thrown off into the blood, which, through their toxin-binding group hinder the access of toxin to the living cell, thereby protecting the cell against injury. This theory, as Ehrlich showed, also applied to problems of cell nutrition. Ehrlich's theory has exerted a profound influence upon research on these problems and it was the dominant conception that guided his work for years.

In 1899 Ehrlich became Director of the newly-founded *Institute for Experimental Therapy* at Frankfurt a.M., and commenced to publish his important researches on *haemolysins* and their mode of action. In haemolysis, according to his theory, amboceptors are cast off by the cells into the blood and serve as factors when coupled with the fermentative complement. This work on haemolysis led directly to Wassermann's discovery of the method of serodiagnosis in syphilis, as Wassermann himself (1915, p. 1105) gratefully acknowledges. In 1904 he published his *Gesammelte Arbeiten zur Immunitätsforschung*, which appeared in English translation in 1906. Erhlich, moreover, conducted important researches on *malignant tumours*, first producing carcinoma in 100 per cent. of his experimentally-inoculated mice so as to proceed from a secure basis of constant production of the malignant growth. His studies related to experimental immunity to mouse carcinoma and to transition forms between carcinoma and sarcoma.

Soon after Ehrlich had become established in Frankfurt, Frau Francisca Speyer became a benefactor to medical science by founding the *Georg Speyer-*

Haus in memory of her husband. This building was erected beside the Institute for Serum Therapy and it was placed at Ehrlich's disposal, thereby facilitating the remarkable researches which occupied him to the end of his life. This, and the naming of a street after him ("Paul Ehrlich Strasse") by the city of Frankfurt attest to the esteem in which he was held by his fellow-citizens.

Ehrlich now plunged into a line of research that was especially congenial to him, namely *systematic investigations on chemo-therapy*. Many years before he had recommended methylene-blue for the treatment of malaria because of its destructive effect on the parasites. He began by attacking *trypanosomiasis* and discovered *trypanred* to be a remedy. He discovered that the trypanosomes in treated animals acquired the power to resist the trypanocidal effect of drugs. He cleared up the chemical constitution of *atoxyl* and made way for systematic work on organic arsenic compounds destined for chemo-therapeutic use. He and his collaborators produced *arsacetin* and *arsenophenylglycin*, which were both trypanocidal, but they were found to exert an unfavourable effect upon the infected host. He next made the brilliant discovery of the *salvarsan* group, including the celebrated preparation "606" which has proved so astonishingly efficient in the treatment of spirochaetal infections and which has since been used throughout the world for the treatment and cure of syphilis. This last discovery was a veritable triumph for Ehrlich, a crowning achievement following upon an enormous amount of systematic labour carried on over a period of many years. Salvarsan has proved efficient in the treatment of relapsing fever, and Framboesia tropica. In the latter instance it has proved so effective that many hospitals could be closed because they were no longer needed for the reception of cases. Moreover, during the war, salvarsan proved trustworthy in the treatment of equine influenza (pink-eye), and even in the treatment of bacterial infections (swine erysipelas, anthrax and glanders), thereby exploding the dogma that pathogenic bacteria in an animal's body cannot be destroyed by drugs. This discovery makes us hopeful regarding what we may expect from future research similar to that launched by the genius of Ehrlich. Finally, continuing his researches, Ehrlich discovered *neosalvarsan*, and, by introducing heavy metals, especially copper, into his salvarsan-complex, he greatly increased the trypanocidal action of this remedy.

During the latter years of his life Ehrlich suffered from progressive arteriosclerosis and therewith connected renal trouble and diabetes. All who knew him, who gave the matter a thought, were convinced that he would not live long. He burnt the candle at both ends, working mind and body to the uttermost limit, year in and year out. He lived in a veritable turmoil of work until close on the end, when he went for reasons of seriously failing health to Bad Homburg, where he died on the 19th of August, 1915. Emil von Behring delivered the oration at Ehrlich's grave on the 23rd.

Ehrlich was an idealist who, regardless of himself, devoted his whole working life to discovering means for alleviating and preventing human

suffering. The Great War came to him as a terrible catastrophe, for, with its advent, he saw all his ideals crumble into dust. There is no question but that the war hastened his death. He had many friends. The loss of his stimulating personality has been felt by all who came within the radius of his genius.

The magnitude of Ehrlich's work can best be gleaned from his *Festschrift*, issued to commemorate his 60th birthday. This work contains a biography, a complete survey of his many-sided scientific activities and that of his associates, a complete bibliography of his published work, besides sections written by many distinguished authors and pupils of the master. A long list of the many papers published by him and his pupils in the *Deutsche medicinische Wochenschrift*, between the years 1881 and 1914, will be found in that journal (1915, p. 1136).

Contrary to Koch, who on the whole avoided scientific controversy, Ehrlich on occasion spoke out sharply. The transparent honesty of the man and his enthusiasm for his work, coupled with the ingenuity with which he built up line after line of defence to guard his theoretical conceptions against aggression, could not but evoke sympathy and admiration even in the ranks of his opponents. In this respect he often reminded me of Metchnikoff in the days when the latter sought to defend his phagocyte theory against attack; he too was deeply sincere and enthusiastic but, because of his highly-sensitive nature, he suffered more in the conflicts upon which he entered. Whatever the antagonistic opinions were or ultimately will be regarding the theoretical conceptions advanced by Ehrlich and by Metchnikoff, they also have this in common that they stimulated thought and the search after the truth throughout the world among workers on immunity. This in itself was a great achievement.

The accompanying portrait of Ehrlich is reproduced from one he gave me in the year 1902; it is an excellent likeness since it conveys a true impression of his quick nervous temperament, whilst in his hands he, in characteristic fashion, holds one of those excellent Havana cigars from which he was rarely parted.

***

The following characteristic letter from Ehrlich is here added because of its exceptional interest. The book referred to in the first paragraph is *Blood Immunity and Blood Relationship*, xii+404 pp. (Cambridge: University Press), published by me in 1904, of which the dedication reads: "This volume is dedicated to *Paul Ehrlich* and *Élie Metchnikoff*, whose genius and influence have greatly advanced and stimulated the search after truth amid the complex problems of immunity." The Nobel Prize for Medicine, to which they were equally entitled, was divided between them in 1908!

GEH. MED. RATH PROF. DR. P. EHRLICH. WESTENDSTRASSE 62,
FRANKFURT A/M., 29. *Februar*, 1904.

Hochverehrter und lieber Freund!

Eben im Begriff, nach Amerika abzufahren, habe ich Ihr Buch erhalten, dessen Widmung mich ausserordentlich erfreut hat. Ich danke Ihnen herzlich für diesen Beweis Ihrer treuen Gesinnung und Anhängerschaft, der mich umsomehr erfreut hat, als ja gerade Sie durch Ihre so erfolgreiche und reiche Arbeit zu einem objektiven Urteil vor so vielen andern befähigt sind.

Ebenso lieb war es mir, dass gleichzeitig das Buch auch Metschnikoff gewidmet ist, zu dem ich, wie Sie ja wissen, auch persönlich in den besten Beziehungen stehe und dessen Leistungen ich ebenso hoch schätze wie Sie. Dass wir in manchen Punkten anderer Ansicht sind, ändert an meiner Verehrung und Liebe für diesen Mann garnichts.

Ich bin jetzt, nachdem Gruber wohl endlich mundtot gemacht[1] sein wird (?) in heftigem Streit mit Arrhenius, der mich eigentlich zu schlecht behandelt hat. Die neueren Arbeiten des Instituts haben mir gezeigt, dass seine unitarischen Anschauungen ganz irrig sind und ich mit meiner eine Pluralität verschiedener Gifte voraussetzende Ansicht doch recht behalte. Ich weiss übrigens auch, dass hervorragende physikalische Chemiker die Beweisführung von Arrhenius auch vom rein theoretischen Standpunkt aus für durchaus nicht beweisend halten.

Mit nochmaligem herzlichem Dank,

Ihr freundschaftlich ergebener

(*facsimile of signature*)

HERRN PROFESSOR DR NUTTALL,
UNIVERSITY OF CAMBRIDGE,
CAMBRIDGE.

The translation of this letter (typewritten, as were all the others received by me) reads as follows:

HIGHLY HONOURED AND DEAR FRIEND!

Just when about to start for America, I receive your book, the dedication of which has given me extraordinary pleasure. I thank you heartily for this proof of your faithful sentiment and attachment which pleases me all the more since you especially, through your so successful and abundant work, are so much more capable than many others to form an objective judgment.

[1] "Mundtot gemacht," as an expression has a charm of its own, meaning literally "made mouth-dead."

PAUL EHRLICH

1854—1915

Equally gratifying to me is it that the book is also dedicated to Metchnikoff, to whom, as you know, I also stand in the best relations and whose contributions I esteem as highly as do you. That we differ in some points does not affect in the slightest my respect and affection for this man.

Now that Gruber has presumably been finally silenced (?), I am in violent conflict with Arrhenius, who really has treated me too badly. The new papers from the Institute have shown me that his unitarian views are entirely wrong and that I with my opinion which assumes the plurality of different poisons am nevertheless right. I know, moreover, that leading physical chemists also regard the evidence produced by Arrhenius as by no means convincing from a purely theoretical point of view.

Again with hearty thanks,

Yours, etc.

REFERENCES.

In writing the foregoing biography I have borrowed freely from the admirable publication by Professor A. von Wassermann (*Deutsche med. Wochenschr.* 1915, pp. 1103–6). See also P. H. Römer (*ibid.* 1914, pp. 521–4, with portraits of Ehrlich and Behring), "J. S." (*ibid.* 1915, p. 1046), and *Paul Ehrlich. Eine Darstellung seines wissenschaftlichen Wirkens* Festschrift zum 60. Geburtstage des Forschers. 668 pp., portrait. Jena: G. Fischer, 1914.

Emil von Behring.

1854–1917.

(Portrait-plate 28.)

EMIL VON BEHRING was born on the 15th of March, 1854 (a day after Paul Ehrlich), at Hansdorf, near Deutsch-Eylau in East Prussia, where he received his early education at the Gymnasium of Hohenstein. He studied at the Army Medical School in Berlin, graduated M.D. in 1878, and passed his State examination in 1880. He then served in the army in Silesia, Posen, and finally Bonn, whither he went in 1887.

Happily for science, as subsequent events proved, Behring had occasion to dress the wounds of soldiers with *iodoform*, a remedy then commonly employed in the treatment of wounds. Iodoform then, and to my recollection for many years afterwards, scented the air of hospitals, German students' duelling grounds and the restaurants and beer gardens in which students congregated with their faces bound up with iodoform dressings. Behring could therefore scarcely escape from the ever-reminding odour of this efficient but disagreeable substance. The efficacy of iodoform was attributed to its directly antiseptic properties until Behring took up the study of its mode of action. He was the first to prove that iodoform modifies the products of putrefaction. In 1882, whilst not denying its bactericidal properties, he laid stress upon the chemical reactions that take place between iodoform and bacterial products. Subsequently he proved that iodoform acts by virtue of its breaking up in contact with the tissues and bacteria, whereby *iodine* is liberated. He argued that the curative action of iodine must depend upon its modifying bacterial products.

At that time Brieger's researches upon ptomaines led many to suppose that ptomaines constituted the essentially toxic products elaborated by bacteria. Behring therefore tested iodoform as against Brieger's cadaverine. He found that iodine lessened the toxicity of cadaverine. Therefore he concluded that remedies for bacterial diseases must be sought among substances capable of neutralizing the poisons of microbes. The conception of *antitoxins*, from now on, floated before his mind.

In 1888 he was ordered to Berlin, but prior to his departure, whilst working in the Pharmacological Laboratory at Bonn, he completed his first studies upon the serum of white rats, which were then regarded as uniformly immune to anthrax. These studies, published in 1888, were directly stimulated by the researches of Fodor (1886), but especially of Nuttall on the *bactericidal properties of serum* (vide Nuttall, *Zeitschr. f. Hygiene*, 1888, IV. pp. 353–94). Behring believed that the bactericidal property of the rats' serum was due to its alkalinity, and consequently that the immunity of these animals was due to the chemical constitution of their serum. Subsequently, however, Behring and Nissen found that the serum of guinea-pigs immunized against *Vibrio metchnikovi* possessed great bactericidal power. It was, however, found that an animal yielding a bactericidal serum was not immune to anthrax and that various pathogenic organisms grew well in corresponding immune sera. Therefore the bactericidal properties of serum did not offer a satisfactory explanation of immunity. Behring now bethought himself of his experiments upon the antagonistic effect of iodine on ptomains and asked himself if immunity did not perchance depend upon the formation in the animal body of an antitoxin for the poison elaborated by the pathogenic microorganism.

At this stage Behring was aided by the discoveries of others. In 1888–90 Roux and Yersin discovered that unheated cultures of the *Bacillus diphtheriae* contained a toxin and soon after K. Faber (1890) and Kitasato discovered that *Bacillus tetani* likewise liberated a toxin. The impulse given by the work of Roux and Yersin was most important in pointing a way to the solution of the problem; they proved, moreover, that the toxin of the diphtheria bacillus was entirely responsible for the pathogenic effects of this microorganism. It was promptly recognized that these bacterial toxins were of an entirely different nature to the ptomaines, of unknown composition and infinitely more potent; nevertheless the discovery of these toxins helped to clear Behring's conceptions regarding the nature of acquired immunity, especially when, in 1890, he and Carl Fraenkel found, simultaneously, that animals could be rendered immune against diphtheria toxin.

Before proceeding I would mention here that Behring became Robert Koch's assistant at the Hygienic Institute, Berlin, in 1889, and that subsequently he worked under Koch at the Institute for Infective Diseases. In 1893 the title of Professor was conferred upon him.

After finding that the serum of guinea-pigs that had been rendered immune to diphtheria bacilli or their toxins, did not kill the bacilli, Behring, in the

summer of 1890, was led to test if the serum had any effect on the toxin of the diphtheria bacillus, and behold it neutralized the toxin! In a paper published on the 4th of December, 1890, was made the important announcement of the discovery of the antitoxins for diphtheria and tetanus (see Behring and Kitasato, *Deutsche med. Wochenschr.* XVI. 1113). Little time had been lost. The initial discovery with diphtheria had been made in the summer, that with tetanus in the autumn. In the latter case Behring worked with Kitasato, the experimental animals being mice. In 1890–93 Behring and Wernicke succeeded in curing small laboratory animals and immunized sheep and dogs against diphtheria toxin; even the sensitive mouse could be cured in the early stages of tetanus infection. By Christmas, 1891, it was possible to make the first trials with diphtheria antitoxin on man, and by January, 1892, the fundamental principles relating to the methods of producing curative sera, their dosage, testing and application had been determined. These developments were influenced by the work of Ehrlich. In 1892–3 the immunization of horses was begun, on the principles established by Ehrlich for the vegetable poisons abrin, ricin and rubin, and in 1894 diphtheria antitoxin could finally be issued to practitioners of medicine for employment in the treatment of diphtheria in man.

Behring's discoveries regarding the value of diphtheria antitoxin were brilliantly confirmed by Émile Roux in 1894. None of us who listened to Roux's masterly exposition that year, at the International Congress of Hygiene and Demography, Budapest, will forget the deep impression engendered by his pronouncement and the enthusiasm it evoked.

After temporarily filling the Chair of Hygiene at Halle in 1894, Behring, in 1895, became Professor of Hygiene and Director of the Hygienic Institute in the University of Marburg. Here he developed extensive laboratories which finally became known as the "Behringwerk," these being destined to forward the application of scientific discoveries in practice. During the Great War large quantities of tetanus antitoxin were issued from the Behringwerk for use in the army. It was not until this war that tetanus antitoxin was used extensively by the contending nations, although the certainty was clearly established years before that it would prove of enormous value. Curiously enough the nations were caught napping in this respect when the war broke out, in consequence of which many valuable soldiers' lives were lost through what should have been avoidable tetanus. In an obituary notice of Edmond Nocard (*Journ. of Hygiene*, 1903, vol. III. p. 519) I wrote of the latter: "His studies on the preventive use of anti-tetanic serum in horses were likewise of great practical and economic importance, and should have a bearing upon the prevention of tetanus in man." Then, and for years after, I urged upon all suitable occasions the employment of the antitoxin on man and occasionally succeeded in having it employed. The matter was so obvious to anyone giving it a thought that it seems incredible for a war to have been required to drive the lesson home. Wernicke, a former collaborator of

Behring's, writing in 1917, actually states that the proof of the great value of tetanus antitoxin in the prevention of tetanus in man was first established through experience gained in the late war.

In tracing the development of Behring's work, we see that he commenced by studying natural immunity and thence proceeded to investigate the causes leading up to the establishment of acquired immunity. He was then able to produce passive immunity, but he was not content with this, he sought to establish the more durable condition of active immunity. His work during the last years of his life concerned itself largely with efforts to establish active immunity against diphtheria in children; he sought to attain this by the administration to them of diphtheria-toxin together with antitoxin. He moreover did an enormous amount of work on tuberculosis which through no fault of his was not crowned with all the success it deserved.

For his discovery of antitoxin Behring was awarded the prize of the Académie de Médecine and Institut de France (1895) and of the Senckenberg Institute of Frankfurt, and he received well-merited recognition from other sources in the form of decorations and of diplomas of universities and learned societies. In 1901 he received the patent of nobility, which entitled him to the prefix *von* before his name, and in the same year he was awarded the Nobel prize. In 1903 he became Privy Councillor and had the title of Excellency conferred upon him by the German Emperor.

After years of illness he died on the 31st of March, 1917, at the age of 63, the cause of death being acute pneumonia. He was buried on the 4th of April in a mausoleum he had himself erected in Marburg.

The accompanying portrait of Behring is reproduced from a photograph obtained from him in 1907 through the kind intermediation of my friend the late Professor Loeffler. It is an excellent likeness.

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Rarely in the history of scientific discovery have the results of laboratory researches been followed so rapidly by their practical application, and few indeed are the workers in the domain of medical science who have in their life-time seen comparable benefits accrue to mankind as a direct consequence of their labours. The discovery of diphtheria antitoxin has saved many thousands of lives throughout the world and robbed diphtheria to a great extent of its terrors, as everyone knows who recalls the tragedies of pre-antitoxin days. Not only was the discovery of immense and immediate practical importance but it stimulated scientific research on immunity to an extraordinary degree and these researches have borne, are bearing, and will bear much fruit. The discovery of serum-therapy by Behring is one of the greatest recorded in the history of medicine since it ranks alongside of the discovery of vaccination by Jenner and of antiseptic surgery by Lister.

EMIL VON BEHRING

1854—1917

REFERENCES.

For a masterly exposition of the progress of scientific research leading up to and following the discovery of antitoxins by Behring, see Chapter I, written by F. Loeffler, in *The Bacteriology of Diphtheria*, edited by Nuttall and Graham-Smith, xx + 718 pp., which appeared in 1908 (Cambridge: University Press). This work contains a full bibliography of Behring's work and that of others dealing with diphtheria, and, in the biographical notice of Behring, given on p. xx, will be found a list of his more important publications. Behring was a much more voluminous writer than Koch. Our portrait of Behring and that of Loeffler which follows, are printed from the same blocks that were used for the portraits that appeared in the above-mentioned work. See also the tribute ("Huldigung") by P. H. Römer, published to commemorate the 60th Anniversaries of Ehrlich and Behring in March, 1914 (*Deutsche med. Wochenschr.* pp. 521–4, with portraits); the highly appreciative tribute by É. Roux and É. Metchnikoff (*ibid.* Sonderbeilage No. 11); the obituary notices which appeared in 1917, from the pens of E. Wernicke (*ibid.* pp. 662–4, with list of publications in that journal during the years 1882–1915), H. Kossel (*Berlin. klin. Wochenschr.* p. 471), M. Mathes (*München. med. Wochenschr.* p. 585), M. von Gruber (*ibid.* pp. 1235–9).

Friedrich Loeffler.

1852–1915.

(Portrait-plate 29, and Facsimile of Letter.)

FRIEDRICH AUGUST JOHANNES LOEFFLER was born on the 24th of June, 1852, at Frankfurt a.O. His father, Gottfried Friedrich Franz Loeffler, was a man of distinction. He did much to raise the status of medical officers in the army, held the position of Sub-Director of the Kaiser-Wilhelm's Akademie für das militärärztliche Bildungswesen, Berlin, attained the rank of Generalarzt with the title of Professor, had the Iron Cross of the 1st Class conferred upon him and, posthumously, a marble bust erected to his memory in the Academy. Friedrich received his early education at Marburg, in the Gymnasium zum grauen Kloster, and in Berlin, at the Collège Royal Français. He studied medicine in Würzburg and subsequently at Berlin, and served as a hospital assistant in the Franco-Prussian war. He took his M.D. in 1874, passed his State Examination in 1875, and was subsequently stationed as a military surgeon in Hanover and Potsdam, where he practised medicine. In 1879 he was ordered to the Imperial Health Department together with Hueppe and Gaffky, and during 1880–84 worked with Robert Koch. In 1886 he became Privatdocent in Hygiene at the University of Berlin, and in 1888 received two calls: to fill the Chairs of Hygiene in Giessen and in Greifswald. He chose Greifswald.

During four years (1903–7) he served as Rector of the University of Greifswald. In 1905 he was raised to the rank of Generalarzt in the Army Medical Corps, and in 1913 succeeded Gaffky as Director of the Institut für Infektionskrankheiten "Robert Koch," in Berlin. During the Great War he served as Generalarzt and hygienist; it was too great a strain for a man of his years, although outwardly he appeared as vigorous as ever. He began to fail

in December, 1914, and was compelled to return in the following January to his home. After much suffering and undergoing an operation which could not alleviate his condition, he died on the 9th of April, 1915. Gaffky relates that Loeffler's mind was occupied with thoughts of scientific problems to the end —even in his delirium. Friedrich Loeffler lies buried in Greifswald.

The importance of Loeffler's bacteriological work, which covered a wide range, may be judged from the following brief summary. In 1882 he (with Schütz) discovered the cause of glanders (*Bacillus mallei*) and described its biological characters. In the same year he discovered the *Bacillus diphtheriae*, described its biology, showed how local is its distribution in the body and indicated that its far-reaching effects were attributable to a diffusible poison, that the procedure to be adopted in treating the disease was to destroy the organisms locally by suitable antiseptics and by seeking means of neutralizing the toxin. This served as a sign-post to Behring in his work that resulted in the discovery of diphtheria antitoxin. Loeffler also discovered the existence of the non-pathogenic *pseudo-diphtheria* bacilli, and the organisms that give rise to diphtheria-like affections in pigeons and calves (1884). In 1885 he discovered the cause of swine erysipelas (*Bacillus erysipelatis suis*), and swine plague (*B. suisepticus*), and, in 1891, *B. typhi murium*. The last, which caused mortality among mice at the Institute in Greifswald, was afterwards used extensively for combating plagues of mice which threatened to destroy the harvests in Thessaly (1882) and elsewhere. Loeffler was the first to show experimentally that animals which have recovered from a bacterial disease (mouse-septicaemia) are immune from a second infection with the same organism that caused the disease, in a manner corresponding to what was known for non-bacterial diseases (smallpox, measles, scarlatina). In 1895, with Abel, he demonstrated the formation of specific protective substances in the blood of animals treated with *B. typhosus* and *B. coli*, and that partially positive reactions may be obtained with non-homologous sera owing to these bacilli being related. In 1897 he was made Chairman of the German Commission for the investigation of *foot-and-mouth disease* and, with Frosch and Uhlenhuth, carried out extensive experiments thereon which were published in a series of reports that appeared during 1897–1905. Loeffler and Frosch were the first to discover, in this connection, the existence in animals of a disease due to a provedly ultra-microscopic virus. Loeffler and his collaborators were able to produce a certain amount of immunity to foot-and-mouth disease in experimental animals by inoculating them with a mixture of recovered-serum plus virus; they hyperimmunized horses and cattle with virus maintained in young pigs, thereby obtaining a protective serum from the treated animals which rendered susceptible sheep, pigs and cattle in a measure immune for some weeks against naturally acquired foot-and-mouth disease.

Bacteriological technique is greatly indebted to Loeffler for many of its standard methods. Every tiro in bacteriology is familiar with "Loeffler's alkaline methylene-blue" which is still universally used, and has heard of

"Loeffler's fagella staining method" (1889–90) if he has not actually employed it. It was Loeffler who introduced meat-juice peptone-gelatin, the malachite-green selective medium for the cultivation of *B. typhosus*, and the method of "enrichment" of the numbers of faecal bacteria prior to isolation in pure culture that is used in all bacteriological laboratories, etc.

Besides the foregoing contributions, Loeffler published numerous papers on disinfection (the first in 1881, on steam disinfection, with Koch and Gaffky), milk hygiene, sewage disposal, the bacteriology of water, besides many reports and contributions on these and allied subjects to learned societies, Congresses and Governments.

In 1887 he published a very valuable work, *Vorlesungen über die geschichtliche Entwickelung der Lehre von den Bacterien* (Leipzig: F. C. W. Vogel), which he had hoped to continue from the date 1878 down to the present time, but other engrossing duties rendered this impossible. This book is a well of information, as its title indicates, on the historical development of the science of bacteriology from remote times down to close on 1881. Likewise in 1887, with Uhlworm and Leuckart, he founded the *Centralblatt für Bakteriologie und Parasitenkunde*, a journal which has flourished ever since.

The value of Loeffler's services was recognized by the conferment upon him of numerous honorary degrees by universities and decorations by Governments of different countries. He was a Privy Councillor and a Member of the German Imperial Council of Health as well as of numerous other bodies.

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Loeffler was the pupil of a number of distinguished teachers of whom may be singled out Reichert, du Bois-Raymond, A. W. Hoffman, Virchow, Traube, Frerichs, v. Bardeleben, v. Langenbeck and Robert Koch. The latter, who was Loeffler's senior by nine years, was called to the Gesundheitsamt in 1880, a year after Loeffler, and until 1884 they were closely associated. Writing of this period (1880–84) in the year 1903, on the occasion of the 60th anniversary of Robert Koch's birth, Loeffler expressed himself with warm appreciation: "The memory of those days, when we still worked in this room, Koch in the centre and we about him, when almost daily new wonders in bacteriology arose before our astounded vision, and we, following the brilliant example of our chief, worked from morn to eve and scarcely had regard to our bodily needs—the memory of that time will remain unforgettable to us. Then it was that we learnt what it means to observe and work accurately and with energy to pursue the problem laid before us." (Fairly literal translation.) The spirit expressed in the foregoing quotation breathed in all the work of Loeffler. His work throughout was characterized by thoroughness and in consequence it has stood the test of time. He published relatively little because he held himself to task until his work on a given theme was as complete as he could make it. A great deal of his work will never see the light because of this. Thus, he carried on researches on immunization against tuberculosis but did

not publish his results because he deemed them inconclusive, although the work had occupied him for years.

He was a man of vigorous physique and great energy, a ready and exceptionally clear speaker whose utterance could be heard distinctly by the largest audience. Under a somewhat rough external manner he bore a modest and kindly nature which endeared him to many.

The accompanying portrait of Loeffler, which is remarkably good, is reproduced from a photograph received from him in 1907.

The following letter from Loeffler was received by me when engaged in editing *The Bacteriology of Diphtheria* in conjunction with my friend Dr Graham-Smith. The letter expresses the writer's regret at his delay in forwarding his manuscript for Chapter I, but, apart from this, the letter is of interest because of its reference to cholera and to the researches he was then conducting on foot-and-mouth disease, a malady that is to-day causing so much havoc in this country.

See facsimile[1] *of letter from Professor F. Loeffler to G. H. F. Nuttall on opposite page.*

GREIFSWALD, *den* 8. *November* 1905.

Hochgeehrter Herr College!

Auf das lebhafste bedauere ich es, dass ich mit meiner Diphtherie Arbeit habe in Rückstand bleiben müssen. Ein unglücklicher Stern hat darüber gewaltet. Als zeitiger Dekan der Fakultät bin ich sehr in Anspruch genommen, meine Maul- und Klauenseuche-Untersuchungen haben viel Zeit erfordert. Ich musste sie auf dem internationalen tierärztlichen Congresse in Budapest vortragen. Nach der Rückkehr wollte ich energisch an die Diphtherie Arbeit gehen. Aber dann kam die Cholera. Material von allen verdächtigen Fällen aus Pommern erhielt ich zugesandt, so dass ich von früh bis spät damit zu thun hatte. Jetzt ist die Cholera vorüber und nunmehr habe ich mich wieder an die Diphtherie-Arbeit gesetzt. Ich bitte nun noch einige Wochen mit mir Geduld zu haben.

Mit freundlichen collegialen Grüssen

Ihr ganz ergebener

(signed) L. LOEFFLER.

Translation:

I greatly regret that I have been obliged to delay my diphtheria work. An unlucky star has hovered over it. At present, as Dean of the Faculty, I am very occupied—my foot-and-mouth investigations have demanded much time. I had to speak of them at the International Congress of Veterinary Medicine in Budapest. On my return, I wished to take up the diphtheria work energetically. But then came the cholera. Material from all suspicious cases was sent to me from Pomerania, so that I was occupied with it from morning till night. Now the cholera has passed and now I have sat down again to the diphtheria work. I beg you therefore to have patience with me for still a few weeks[2].

[1] Reduction by 1/3 [2] MS. received 16th January, 1906

Greifswald, den 8 November 1905.

Hochgeehrter Herr Collège!

Auf das liebenswürdigste bedauere ich es, dass ich mit meiner bisherigen Arbeit hier im Rückstand bleiben musste. Ein ungleich grösserer Stoss hat darüber gewuchert. Als geistiger Leiter der Fakultät bin ich sehr in Anspruch genommen, meine Assistenten Klausurarbeiten haben viel Zeit erfordert. Ich werde sie auf dem internationalen tierärztlichen Congresse in Budapest vortragen. Und an Bücherei wollte ich energisch an die bisherige Arbeit gehen über dem Haus der Chaîne. Nehmen Sie allen verdienstigen

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Fleiss aus Pommern anbelangt, so bin ich vor Freude bis spät damit zu thun hatte. Jetzt ist die Chaîne vorüber und genommen habe ich meine wieder an die bisherige Arbeit gesetzt. Ich bitte nun noch einige Wochen Geduld zu haben.

Mit freundlichen Grüssen

Ihr ganz ergebenster

F. Loeffler

REFERENCES.

In writing the foregoing biography of Loeffler, I have referred to original notes and publications besides the following sources of information: (*a*) *Medicinisches Deutschland* (Berlin-Charlottenburg: Adolf Eckstein, 1902), a reprint from the folio volume having been sent to me by Loeffler in 1907, with numerous MS. additions up to that date. (*b*) *The Bacteriology of Diphtheria*, edited by Nuttall and Graham-Smith (Cambridge: University Press, 1908), where the portrait here reproduced first appeared. (*c*) Notices that appeared in 1915 from the pens of Abel (*Centralbl. f. Bakteriol. u. Parasitol.* Orig. vol. LXXVI. pp. 241–5) and G. Gaffky (*Deutsche med. Wochenschr.* pp. 393–5, with portrait).

FRIEDRICH LOEFFLER

1852—1915

THE ABSENCE OF PAEDOGENETIC MULTIPLICATION IN THE BLOW-FLY (*CALLIPHORA ERYTHROCEPHALA*).

By D. KEILIN, Sc.D.,

Beit Memorial Research Fellow.

(*From the Molteno Institute for Research in Parasitology, University of Cambridge.*)

(With 3 Text-figures.)

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I. Paedogenesis in Insects.

Paedogenesis, or the multiplication of an animal in its immature stages of life, is a very rare phenomenon and is known to occur only in a few species of holometabolic insects.

In the year 1861, N. Wagner, then Professor at the University of Kazan (Russia), discovered in the stumps of various trees colonies of small larvae, each of which harboured within its body-cavity a number of daughter larvae. These ultimately made their escape, leaving behind the empty skin of the original larva and, soon after obtaining their freedom, they developed within their body-cavities another generation of larvae, this process of multiplication continuing repeatedly throughout the autumn, winter and spring. In the summer, however, the larvae ceased to multiply but were transformed into pupae, which developed into adults, male and female, in the normal manner.

When first announced, this phenomenon was considered to be so improbable that Wagner's discovery was received with scepticism by such leading zoologists as von Baer, von Siebold and Brandt, and it was not until a year later, when Owsiannikow brought from Kazan to Petrograd a log of wood harbouring these exceptional larvae and demonstrated their mode of propagation, that a prize was awarded to the discoverer.

Soon after this, Wagner's observations were confirmed by several zoologists in various parts of Europe and in America. The larvae were found by Meinert

(1864) and identified by him as belonging to a Cecidomyid fly which he named *Miastor metraolas*. Pagenstecher (1864) found the larvae in Heidelberg, Ganin (1865) in Charkoff, Leuckart (1865) in Giessen, Kahle (1913) near Leipzig, and Felt (1911) in America. I have found these larvae near Paris on several occasions, and also in Cambridge, inhabiting old stumps of elm and horse-chestnut trees on the Downing site.

Among the Diptera, two other cases of paedogenetic multiplication have been observed, the one by Grimm (1870) in an unidentified Chironomid, probably a *Tanytarsus*, and the other by Zavřel (1907) in *Tanytarsus boiemicus* Kieffer. These cases differ from that of *Miastor* in that the phenomenon occurs in the fully-developed pupae only, which produce ova parthenogenetically, whence normal larvae hatch.

In 1913, a remarkable example of paedogenetic multiplication was discovered by Barber in a beetle—*Micromalthus debilis*. The paedogenesis in this insect is complicated by an extraordinary larval polymorphism, with the coexistence of oviparous and viviparous paedogenetic larvae.

Until recently our knowledge of paedogenesis in insects was restricted to the three above-mentioned cases, but recently, Parker (1922) claimed to have discovered the existence of a possible paedogenetic propagation in the common Blow-fly (*Calliphora erythrocephala*). Considering the rarity of the phenomenon in general, any new case of paedogenesis is sufficient in itself to arouse interest, but when it happens in such a familiar insect as the Blow-fly, living in close association with man, it assumes a paramount importance. Moreover, the data relating to the multiplication of the common Blow-fly and of all the allied forms of Calliphorine flies, are of special importance, as these flies are known to be the cause of cases of widespread and injurious myiasis in man and domestic animals.

It would be a matter for great surprise if this phenomenon had escaped the notice of the many zoologists who have had occasion to work on the various problems connected with the Blow-fly. For many different purposes I myself have had occasion to dissect hundreds of these larvae without ever encountering a single indication of their paedogenetic reproduction, and was inclined, at first, to doubt the correctness of Parker's observations or the soundness of his experiments. On the other hand, the history of Wagner's discovery affords a sufficient warning against the mistrust of the statement of a zoologist, merely because his assertions are extraordinary, and it seemed to me that the only course for me to take would be to repeat Parker's experiments.

II. Parker's Experiments on Blow-Flies.

In the early autumn of 1918, while working with cultures of *Calliphora erythrocephala*, Parker noticed that the numbers of maggots in his cultures seemed to exceed the number of eggs originally introduced. His preliminary experiments (25. xi. 1918), by which he attempted to prove his assumption, proved to be defective in method, and were dropped as inconclusive. In the

spring of 1919 he elaborated an improved technique which may be described as follows:

"Fifty clean quart jars were prepared by pouring into them enough coarse sand to cover their bottoms. This sand had previously been sterilised by baking. Into each jar was then introduced a small glass beaker containing a bit of carefully inspected fish meat. The jar was then closed by having mosquito netting tied over its open end and by setting in place of this netting the glass cover of the jar without, however, clamping it down. Thus it was believed that the jars were effectively protected against the introduction of eggs from the outside and that the gases generated by the decomposing meat within could escape....The fish meat in the jars was not sterilised by cooking, for it was found to decompose much more freely and satisfactorily when uncooked."

Using this method, he conducted several experiments during April, May and June, 1919, but he obtained negative results—*i.e.* he failed to detect any increase in the number of the larvae.

In the autumn of 1919, by isolating a definite number of eggs, Parker found that in *Calliphora*, there is no polyembryonic multiplication, each egg giving rise to one larva only. In October and November of the same year he repeated the experiments which he had carried out in the spring and early summer, and this time obtained the following results. On October 2nd he set up fifty jars with fish meat. These, examined twenty-six days later, showed no maggots to be present. The following day a freshly-hatched maggot of *Calliphora* was placed in each of the twenty-five jars; the remaining jars were left uninfected to serve as controls. On November 10th the twenty-five control jars still contained no maggots, while of the twenty-five infected jars, three contained no larvae, twenty jars contained one maggot in each, one jar held eight maggots and one jar twenty-one maggots.

This experiment was repeated on October 8th. Fifty jars were set up as before with fish meat. Examined on November 15th, they were found to be free from maggots and, on the same day, twenty-five jars were infected with a single maggot each, and the remaining twenty-five jars retained empty as controls.

An examination on November 26th showed the control jars to be still free from larvae or pupae of *Calliphora*, while of the twenty-five infected jars, six contained no larvae, eighteen contained one pupa in each, and one jar contained seven pupae.

From these experiments Parker drew the following conclusions: "The tests of October 2nd and October 18th were carried out with such precautions that it seems impossible that the results could be due to accident. The increases observed have always occurred in the autumn and never in the spring and I am therefore led to believe that in October and November, or even later, *Calliphora erythrocephala* occasionally multiplies in an unusual way, and that this way is not polyembryony but paedogenesis."

Before proceeding to a description of my own experiments, I would call attention to the fact that Parker's conclusions are based on two experiments only, dealing in all with fifty larvae, of which nine died, thirty-eight remained single and did not multiply, while the remaining three he believed to have multiplied, producing respectively seven, eight, and twenty-one larvae.

III. Personal Observations and Experiments on Blow-Flies.

To detect a paedogenetic multiplication in an insect the simplest method of procedure is to examine or to dissect a number of the larvae during a period when this kind of multiplication may be expected to occur. During the months of October, November and December I dissected 148 larvae of *Calliphora erythrocephala* without discovering the slightest indication of paedogenetic multiplication.

My next procedure was to breed a definite number of larvae from the egg to the pupal stage, with the object of determining whether or not there was any increase in number. In carrying out such experiments, the avoidance of accidental infection of the cultures is by no means so easy as might be supposed. All who have worked with Calliphorine flies realise how difficult it is to protect cultures of their larvae from the intrusion of larvae derived from without. A flask or culture tube, firmly plugged with cotton wool, and safe from bacterial contamination, affords poor protection of the contents against the invasion of Calliphorine larvae. The adult flies are attracted by the smell of the decomposing food material which diffuses through the cotton wool plug of the flask, and, if the flies cannot reach the contents of the flask directly, they oviposit on the plug, and the young larvae quickly make their way through it and so reach the interior. Gauze covers, corks and even glass plates are unreliable for the effective closing of the culture vessels. The small larvae hatch out within 24–48 hours of oviposition, and will squeeze their way through the most minute apertures in order to reach the decomposing culture medium upon which they thrive. The eggs of *Calliphora* are of fairly large size and easily seen and even counted when lying upon a clean glass surface or a dark background. When deposited on cotton wool or white gauze, however, they are not so visible and may easily be overlooked. In the breeding experiments, therefore, cotton wool or gauze, wholly or partially exposed to the exterior, is to be avoided. Although the young larvae are very resistant, and able to pass through almost any barrier, they are unable to make their way through any considerable quantity of water, and this affords a means of interposing a very efficient barrier against intruding larvae.

Experiments I–IV. The first experiments were commenced on September 28th. Slices of cooked beef were introduced, while still hot, into Erlenmeyer flasks. These were then placed, in groups of five or seven, in a dish filled with water and covered with a bell-jar, the lower edge of which was immersed in the water. Two glass tubes, bent into an ∩-form and inserted under the rim of the jar, allowed for communication between the inside and the external air.

Experiment V. The Erlenmeyer flasks were replaced by ordinary test-tubes, standing in a rack and leaning against each other.

After allowing the meat to cool, a number of eggs of *Calliphora erythrocephala* was introduced into each flask or tube. The contents of each flask were examined on October 8th, and the results are tabulated below.

Exp. No.	No. of flasks or tubes put under each bell-jar	No. of eggs put in each flask or tube	Total No. of eggs put under each bell-jar 28. ix. 1923	Total No. of full-grown larvae found on 8. x. 1923
I	5 flasks	5	25	24
II	6 ,,	10	60	53
III	7 ,,	10	70	69
IV	6 ,,	10	60	58
V	23 tubes	5	115	114
		Total	330	318

None of the flasks (Exps. I–IV) contained more larvae than the original number of eggs. In Exp. V, on the other hand, where the tubes were touching each other, the number of larvae in some of the tubes was greater than that

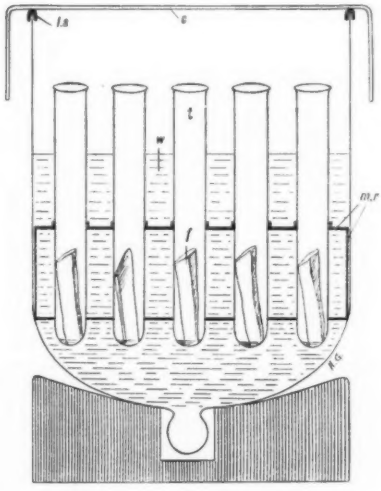

Fig. 1. Optical section of a breeding jar used in Exps. VI–XIII. *c.* glass cover, *f.* food, *l.s.* lead strips, *m.r.* metal rack, *t.* test-tubes, *w.* water.

of the previously placed eggs, but this was due entirely to the migrations of the larvae, which were actually seen to pass from one tube to another. In all the bell-jars the number of full-grown larvae obtained was lower than the original number of eggs, the loss being due to a natural mortality, the rate of which (about 3·6 per cent.) was exceptionally low.

Experiments VI–X. In these experiments I modified the method previously employed in order to comply with the following requirements: (1) avoidance of infection from the exterior, (2) prevention of the migration of larvae from one tube to another, and (3) the provision of a compact form of apparatus for the breeding of a reasonably large number of single larvae. For this purpose I used an inverted bell-jar (Fig. 1) containing water (*w.*), and a rack (*m.r.*) formed of two parallel discs of sheet lead, connected by

three vertical strips of galvanised iron. In each of the discs, a number of holes was punched, of a size suitable for the reception of test-tubes of ordinary dimensions (*t.*). Each test-tube was fitted with a short sleeve of sheet lead to act as a sinker. The mouth of the bell-jar was covered with a shallow glass dish (*c.*), supported upon three strips of lead (*l.s.*), one millimetre thick, and bent over the edge of the bell-jar, so as to leave an opening sufficient for ventilation.

On October 10th five of these fitted bell-jars were arranged, and a slice of cooked meat (*f.*), with a single newly-hatched larva, was introduced into each test-tube. The jars were kept in a room free from flies, and their surfaces carefully examined three times a day for the presence of eggs deposited by roving flies. A single egg of *Calliphora* laid on any part of the breeding jars would then be easily noticed and removed before it had time to hatch. From October 18th to 20th the contents of the test-tubes were examined by emptying them separately, with the results as shown in the following table.

Exp. No.	No. of tubes per jar	No. of tubes with one full-grown larva on October 18th–20th	No. of tubes without larvae
VI	19	18	1
VII	18	14	4
VIII	18	11	7
IX	20	19	1
X	21	20	1
Totals	96	82	14

Experiments XI–XIII. Similar experiments to the last were carried out in November, cooked fish being used in Exps. XI and XII, and a mixture of raw fish with cooked sheep's brain in Exp. XIII. The food material was introduced into the tubes and allowed to stand from the 9th to the 15th of November. No accidental infection had occurred, and then, on November 15th, a single newly-hatched larva was introduced into each tube. The contents of the tubes were examined on November 22nd, with the following results.

Exp. No.	No. of tubes per jar	No. of tubes with one full-grown larva on November 22nd	No. of tubes without larvae
XI	21	21	0
XII	22	21	1
XIII	21	20	1
Totals	64	62	2

Experiment XIV. A slightly modified method was used in this experiment. In a large bell-jar (Fig. 2) a disc of galvanised iron (39 cm. in diam.) was immersed in water (*w.*). On the upper side of this disc twenty-four cylindrical boxes had been soldered (*m.b.*). The boxes, which measured 5 cm. by 5 cm. were then filled with sand (*s.*), into which short glass tubes (*f. t.*) containing the food

material were inserted. The mouth of the bell-jar was covered with a sheet of plate glass (*c.*) which was allowed to rest on three strips of sheet lead (*l.s.*) bent over the edge of the jar.

On November 9th the tubes were filled with raw fish and left until the 15th, when a single newly-hatched larva of *Calliphora* was introduced into each tube. On the 26th the contents of each tube were examined, together with the surrounding sand. Three of the boxes were found not to contain larvae, these having died, in all probability, in an early stage. In each of the remaining boxes a single full-grown larva or pupa was found.

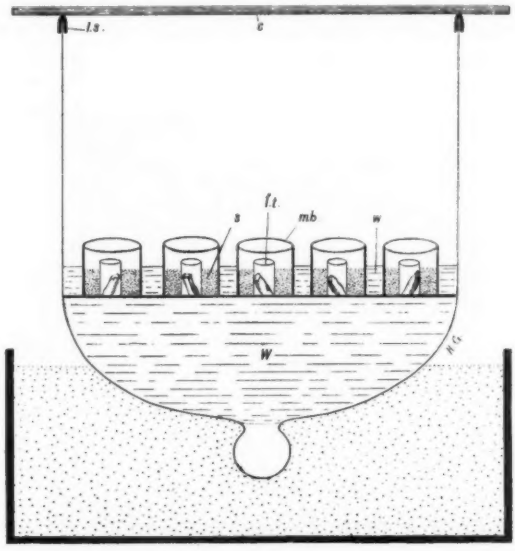

Fig. 2. Optical section of a breeding jar used in Exp. XIV. *c.* glass cover, *f.t.* feeding tube, *l.s.* lead strips, *m.b.* metal box, *s.* sand, *w.* water.

All these experiments clearly demonstrate that there is no sign of paedogenetic multiplication in *Calliphora erythrocephala*[1].

Throughout the series of experiments the bell-jars were kept, so far as was possible, in rooms free from flies.

Experiments XV–XVI. It remained, therefore, to ascertain to what extent the breeding contrivances would afford protection from outside infection. With this object in view, two bell-jars (as in Fig. 1) were set up on November 9th, one with twenty-three test-tubes containing fish and brain (Exp. XV), the other with twenty-two test-tubes containing fish and brain (Exp. XVI). The bell-jars were then placed in a room with free *Calliphora* flies. On the

[1] The full-grown larvae obtained in these experiments were put into moist sawdust and two to three days later were transformed into the pupae. The number of the adult flies (♂ and ♀) hatched from these pupae was always equal to that of the larvae.

14th eggs were found on the inner surface of the walls of the bell-jars, 150 eggs in Exp. XV (Fig. 3), and about 20 in Exp. XVI. While unable to enter the bell-jar, the fly had been able to insert its ovipositor through the narrow space between the rim of the jar and the glass cover and so lay its eggs on the inner surface of the jar. Subsequently the larvae hatched and were found wandering upon the walls of the jar. On November 23rd the tubes and jars were carefully examined. No larvae were found in any of the 45 tubes of the two jars, but 141 and 8 first-stage larvae respectively were found drowned in the water of the two jars. Not one of the 170 first-stage larvae which had been observed wandering on the walls of the jars had succeeded in reaching any of the 45 food-containing tubes. In other words, the water barrier had prevented the infection of the tubes from without.

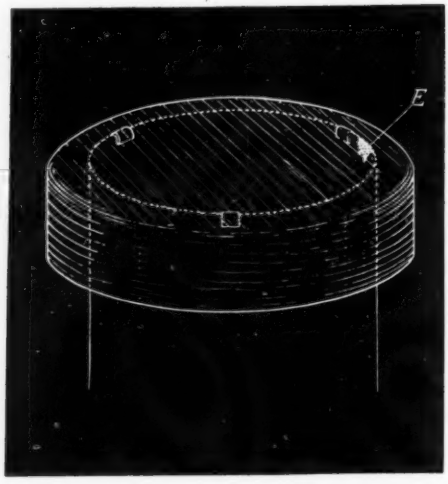

Fig. 3. Upper portion of a breeding jar as in Fig. 1, showing egg mass—*E*—laid by a *Calliphora* fly upon the inner surface of the rim of a bell-jar (Exp. XV).

IV. Conclusions.

Dissections and breeding experiments, involving the examination of 661 larvae, have clearly proved that neither paedogenesis nor polyembryony occur in the larva of *Calliphora erythrocephala*, and that Parker's assumptions have been derived from faulty experiments. The apparent increase in numbers of the larvae in some of his experiments was due, not to the multiplication of the larvae, but to fresh infections of his culture media from external sources.

The outstanding defects of his method were (1) the use of too small a number of larvae, far-reaching conclusions being based upon experiments with not more than 50 larvae in all, (2) the use of mosquito netting or gauze, which

is not necessary for the prevention of accidental infection and which conceals the eggs which roving flies deposit around the lid of the jar, and (3) failure to employ an effective barrier (*e.g.* water) against larvae, which, after entering the culture jar, seek access to the culture tubes.

My thanks are due to Mr Charles Harpley, our chief laboratory assistant, for his valuable help in constructing the apparatus used in the experiments and for sharing with me the discomfort which such experiments involve.

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(*MS. received for publication* 7. I. 1924.—Ed.)

THE ANOMALOUS POSITION OF PARASITOLOGY IN THE MEDICAL CURRICULUM IN ENGLAND.

By GEORGE H. F. NUTTALL, F.R.S.

Although Parasitology, broadly interpreted, includes the study of parasitic bacteria within its sphere, bacteriology is excluded from consideration here because it is assumed that a knowledge thereof is sufficiently recognised as essential by those who deal with medical education. At any rate bacteriology is more or less adequately taught to medical students and candidates for the Diploma in Public Health, although it receives insufficient consideration in courses leading to the Diploma in Tropical Medicine and Hygiene. On the other hand, parasitology is taught to candidates for the latter diploma to the limited extent that is allowed in the too short courses of instruction that are at present given for the diploma. Medical students in general learn next to nothing of parasitology beyond what they pick up in the course of their preliminary zoological training. I base these statements on personal experience, extending over many years, as teacher and examiner. Similar conclusions to these have been reached by others who are able to form an objective opinion.

Gross ignorance of the elements of parasitology prevails in the profession. To substantiate this statement, the following instances may be cited from personal knowledge or that of trustworthy witnesses among my acquaintance:

(1) The symptoms of *common helminthic affections* especially in children are frequently not recognised and their treatment not understood. Cases of gross ignorance in this respect are of common occurrence.

(2) The technique required in the collection of samples of *faecal discharges* and their examination for parasitic worms and their ova or dysentery amoebae is altogether insufficiently known.

(3) The widespread inability to diagnose *scabies* or itch by finding the mite (*Sarcoptes scabiei*) and prescribing or following the curative treatment intelligently was sufficiently evident during the war for many of us to have cognizance of it.

(4) In a certain hospital some 60 cases were diagnosed as *malaria* and treated as such. The *blood-films* were badly prepared and badly stained and various artifacts and precipitates had been taken for parasites. Mistakes of the kind are frequent, though unusual, on such a scale.

(5) The diagnosis of *filariasis* has been repeatedly made in consequence of cotton-fibres being mistaken for microfilaria in stained blood-films, the fibres having been derived from cotton pledgets that had been used for cleansing the skin prior to pricking it to draw blood for film making.

When we consider the candidates for the Diploma in Public Health alone, we obtain ample evidence of inadequate training in parasitology and the trustworthy letter that follows, recently received by me in my capacity of editor of *Parasitology*, amply shows that in some institutions the training of

such candidates in parasitology is reduced to a mere farce. What the writer of the letter states regarding medical entomology, for it is to this limited part of parasitology that he confines himself, applies equally to the subject as a whole in respect to present day methods of teaching and examination in some institutions.

8th January, 1924.

THE EDITOR, *Parasitology*.

SIR,

The new regulations of the General Medical Council relative to the D.P.H. curriculum necessitate many changes in the course of instruction and examination for this qualification. I wish to point out the necessity for ensuring that prescribed subjects such as medical entomology will be systematically taught, and further, that the examiners within whose province medical zoology falls will have a competent knowledge of the subject. This will doubtless seem a hard saying to some, but painful experience proves it is amply justified. I can best support my contention by describing the "Practical Medical Entomology" given at one teaching institution as part of the D.P.H. course. The instruction in this subsidiary subject was allotted to a junior member of the hygiene staff as an addition to his own proper duties, in which he was highly proficient. Fortunately he possessed a sense of humour and acknowledged cheerfully and frankly that the course of medical entomology was "an absolute farce." "I know nothing about the subject," he told me, and added with a twinkle in his eye, "but neither do the examiners, and this is the sort of stuff that goes down with them." The class then commenced the study of fleas. The instructor warned them that they must be familiar with three fleas—*P. irritans*, *X. cheopis* and *C. fasciatus*. *P. irritans*, he explained, is darkish in colour, and much larger than the low power field of the microscope. *X. cheopis* is lighter in shade and smaller. Whereas *C. fasciatus* has a row of black teeth on the "neck." A demonstration of these characters disposed of the Siphonaptera, and the class proceeded next to study flies. The instructor informed them that any small dull coloured fly would certainly be either *M. domestica*, *F. canicularis* or *S. calcitrans*. The first is characterised, he said, by a sharply angulated 4th vein, the second by a straight 4th vein, and the last by its projecting proboscis. The students demonstrated their ability to recognise these points, and I observed with interest that some of the specimens of "*M. domestica*" shown did not belong even to the Muscidae! And so the farce continued. Not one of the class could have defined an insect, or had they even a hazy idea of the conceptions expressed by such terms as Order, Family and Genus. Yet they "identified" species with all the confidence of ignorance, and seemed to believe that they really could recognise the insects named so glibly.

In fairness I must add that the teaching in bacteriology, hygiene, etc., was excellent, and the standard of knowledge in these subjects was very high. The instructor told me that his candidates were "always asked something about insects" in this examination, and that they experienced no difficulty in satisfying the examiner responsible. From this one can only assume that no marks were allotted to the subject. Such a condition of things appears to affect medical zoology only. In no examination in bacteriology, however elementary, would one find a candidate naming, say, *B. typhosus* on the evidence of a stained smear. If he did, swift retribution would follow. Yet students are actually taught to commit equally heinous crimes in the identification of animal parasites and escape unscathed.

However profound an examiner's knowledge of pathology or hygiene may be, he brands himself as ignorant of the elements of parasitology by accepting a diagnosis of say, *X. cheopis*, from a candidate who could reasonably be expected only to recognise the specimen as a flea, and to name a few of its more obvious characters. I do not mean to infer that all institutions which include parasitology in the D.P.H. curriculum teach the subject in the scandalous fashion described above, nor do I doubt that some bodies granting this diploma may include amongst their examiners someone conversant with medical zoology. But I do assert that in at least some cases a working knowledge of parasitology is an actual handicap to a candidate for he is unable to venture beyond, perhaps, an Order or Family, while his

more ignorant competitors rattle off the specific names, which seem to be expected, or at any rate tolerated, in such examinations.

I am, Sir,

Yours obediently,

"X."

What are the remedies for the lamentable state of affairs described in the foregoing paragraphs and letter?

Obviously parasitology requires to be *adequately taught* in the curriculum of our medical schools (I would note that in France the course extends over no less than a year for all medical students). To accomplish this trained teachers are required. Secondly there is a lack of *competent examiners*, the few there are belonging mostly to the staffs of schools of tropical medicine.

Teaching and examination in parasitology cannot be conducted otherwise than improperly by those who have an inadequate knowledge of the subject. It is obviously absurd to relegate such an important subject to any stop-gap hygienist or bacteriologist, however competent he may be in his sphere. If a bacteriologist is required as teacher or examiner in bacteriology there is fully as good reason why a parasitologist should perform corresponding functions with regard to his subject. There are very few, if any, capable of fulfilling both functions. Parasitology in relation to man, leaving animals almost out of consideration, has made great strides in recent years, and much more detailed and varied knowledge is required than appeared adequate a couple of decades ago. To-day we have to deal with a multiplicity of organisms: Arthropods (Insecta, Acarina, Crustacea, which serve either as vectors or hosts of parasites, or are of themselves parasitic), Helminths (Nematoda, Trematoda, Cestoda, many new forms of which have become known together with their life-histories), Protozoa (many developments of recent years), Fungi other than Bacteria (not adequately considered anywhere in this country), the spirochaetes and the ultramicroscopic or filterable viruses (as likely as not to be omitted from bacteriological courses or to receive inadequate attention). Lastly, frequently saddled upon a course in parasitology, we have what may be strictly termed medical zoology which deals with venomous or noxious animals.

It is impossible to give a course of instruction so complete that candidates for degrees or diplomas shall become adepts in all branches of parasitology, but at least they should learn how to collect, preserve or prepare any material that comes into their hands and which may have to be dealt with by experts. At present the prevailing ignorance is so great that any material, even blood-films and specimens of discharges, etc., are rarely received by the expert in a fit condition for satisfactory examination.

Surely it is time for all intelligent persons to realize that parasitology requires a status of its own. In the first instance this recognition should come from those in authority: from those who should realize their responsibility when they come to appoint teachers and examiners and from those who frame courses leading to examinations intended to fulfil modern requirements.